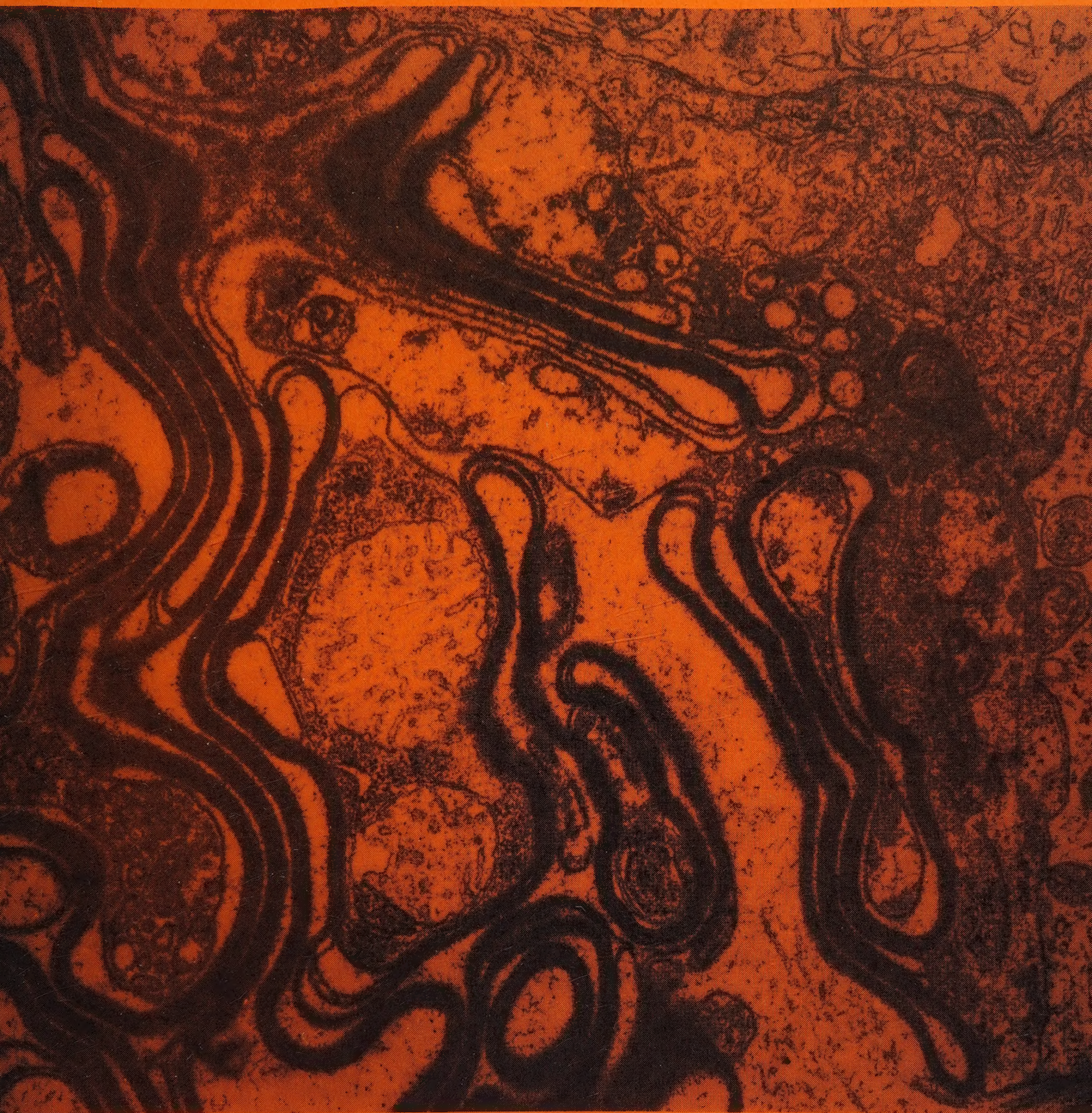


THE ORGAN OF BELLONCI



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LUND 1976

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The thesis comprises the following papers:

- I The fine structure of the organ of Bellonci in the Crustacea Maxillopoda, especially Balanus improvisus Darwin (Maxillopoda Cirripedia) and Derocheilocaris remanei Delamare and Chappuis (Maxillopoda Mystacocarida). - Kauri, T.
- II The structure of the organ of Bellonci of the syncarid crustacean, Anaspides tasmaniae (Thomson). - Kauri, T. and Lake, P.S., Z.Zellforsch. 132: 431-450 (1972).
- III Fine structure of the organ of Bellonci (SPX) in Boreomysis arctica (Krøyer) (Crustacea, Mysidacea). - Kauri, T. and Dahl, E., Zool. Scr. 4: 41-47 (1975).
- IV The fine structure of the organ of Bellonci in Diastylis rathkei Kr (Crustacea, Peracarida, Cumacea). - Kauri, T.
- V Observations on the fine structure of the organ of Bellonci (SPX) in Halice abyssii BOECK (Crustacea, Peracarida, Amphipoda). - Dahl, E. and Kauri, T.

Of these papers those in manuscript, viz I, IV, and V, are presented here.

A summary is presented separately.

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The fine structure of the organ of Bellonci in the Crustacea Maxillopoda, especially Balanus improvisus Darwin (Maxillopoda Cirripedia) and Derocheilocaris remanei Delamare and Chappuis (Maxillopoda Mystacocardia).

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Abstract

The fine structure of the cephalic receptors in B. improvisus and D. remanei is described. In the former the structural characteristics of the proximal component of the frontal filament complex compare favourably with those of the cephalic organ of the latter and with those of the corresponding cephalic organs of the Copepoda. This organ in the Maxillopoda is homologized with the oB. The distal component of the frontal filament complex in Balanus is compared with the corresponding organs in the Copepoda and their homologies are discussed. In Balanus the structural characteristics of the cephalic receptors during the moulting cycle are briefly described, and in Derocheilocaris the functions of individual elements of the oB are discussed.

Introduction

Several descriptions of the fine structure of cephalic receptors among the Maxillopoda have appeared during recent years.

Copepoda. Among the Calanoida three different units have been described, corresponding to what previously was known as frontal organs and x organs, in Calanus finmarchicus, Euchaeta norvegica, Chiridius armatus, Sapphirina angusta, S. auronitens, and S. ovato-lanceolata (Elofsson, 1971).

In the Notodelphyidae two presumed sensory units have been described in nauplius and copepodid stages of Doropygus seclusus (Dudley, 1972).

Cirripedia. The frontal filament complex in larvae of the thoracicans Balanus balanoides, Elminius modestus, and B. hameri have been described (Walker, 1974).

A cephalic organ has also been briefly described (Elofsson, 1971) in Hansen's nauplius Y, which larva is believed to belong to a species of either the Ascothoracica (Bresciani, 1965) or the Cirripedia (Elofsson, 1971). Adults are as yet not known. The Ascothoracica are closely related to the Cirripedia, but might be considered as an independent order (Wagin, 1946).

Earlier work on structures in the cephalic region has been reviewed for the Copepoda (Elofsson, 1963, 1965, 1966; Dahl, 1965; Dudley, 1972), and the larvae of Cirripedia Thoracica (Kauri, 1962; Walley, 1969; Walker, 1974). Cephalic organs in the larvae of Cirripedia Acrothoacica and Rhizocephala and of the Ascothoracica have been briefly described (Kauri, 1966).

In the Mystacocarida cephalic organs have been described and discussed (Dahl, 1952; Elofsson, 1966; Baccari and Renaud-Mornant, 1974).

In the Branchiura cephalic organs other than the nauplius eye have not been recorded (cf. Elofsson, 1966).

The Apoda finally, earlier included among the Cirripedia, have been reevaluated (Bocquet-Védrine, 1972) and their only representative, Proteolepas bivineta, identified as a developmental stage of the Isopoda Cryptoniscida.

Among the cephalic organs described from these species probable homologues to the organ of Bellonci (oB) have been found. Homologizations have been attempted in the Cirripedia Thoracica (Kauri, 1966) and Copepoda Calanoida (Elofsson, 1971).

Another cephalic organ, found in the Copepoda and possibly in the Cirripedia, is compared to the cavity receptor organ, described from the Anostraca (Elofsson and Lake, 1971), while a third cephalic organ is known only from the Copepoda (Elofsson, 1971).

The present examination of the fine structure of the cephalic receptors in B. improvisus and D. remanei was undertaken in the course of a comparative study of the oB in the Crustacea. The observations on the frontal filament complex in larvae of B. improvisus are given mainly to add information on the fine structure during the moulting cycle, but also to add new information on the organ complex generally in addition to the work by Walker (1974).

Material and method

The larvae of B. improvisus were collected from the Sound (between Sweden and Denmark) with a simple plankton net and brought to the laboratory. Specimens of V and VI stage nauplii were decapitated under 2,5 % glutaraldehyde and fixed in same (60 min). Postfixation was carried out in 1 % OsO_4 (60 min).

Both fixatives were buffered to pH 7,3 with phosphate buffer (Millonig, 1961). The glucose was omitted from the fixative. The specimens were dehydrated in an ethanol series and additional contrast was added through immersion in a solution of 0,5 % uranyl acetate and 1 % phosphotungstic acid in absolute ethanol. Embedding was carried out in Vestopal W and sections were cut on an LKB Ultratome 8801 A. The sections were examined on formvar-coated hoenycumb grids in Philips EM 300 and Zeiss EM 10.

Specimens for the scanning electron microscopy were dehydrated in an acetone series, and via amyl acetate brought to critical point drying in CO_2 . The drying apparatus used was a modification of that described by Boyde and Wood (1969).

The individual specimens of a stage were arranged in a series according to age as judged from the appearance of the cuticle and the processes from epidermal cells underlying it (Fig 11, 12, 13). The majority of the specimens were in an intermediate phase of the moulting cycle (Fig 13), but a few early phases (Fig 11) and two specimens undergoing apolysis (Fig 12) were examined.

The material of D. remanei was obtained from Canet - Plage east of Perpignan (France) and brought to the laboratory alive.^{x)} The specimens were fixed in toto and the fixation, embedding and examination procedures were the same as for the barnacle larvae.

^{x)} I am indebted to Drs P.H. Enckell and L. Hagerman for collecting the material and bringing it to our laboratory in Lund.

The frontal filament-oB complex in the Cirripedia is present only in the larval stages (Kauri, 1962; Walley, 1969; Walker, 1974). It is situated anteriorly in the larva with the oB in a proximal position to the point of origin of the frontal filament (Fig 3).

The oB

The frontal filament-oB complex is supported by a small number of cells. These supporting cells have their perikarya around the oB (Fig 3). Processes from these cells delimit the organ cavity, establish contact with the epidermal cells distally and also enter the basal part of the frontal filaments (Fig 3, 11). Further elements to the oB are contributed by dendrites from the nerve to the complex. The dendritic terminals carry pairs of cilia. The nerve originates from bipolar neurones in the protocerebrum (Kauri, 1962). About four dendrites penetrate into the oB cavity while more than a dozen dendrites bypass the organ laterally and continue to the filament.

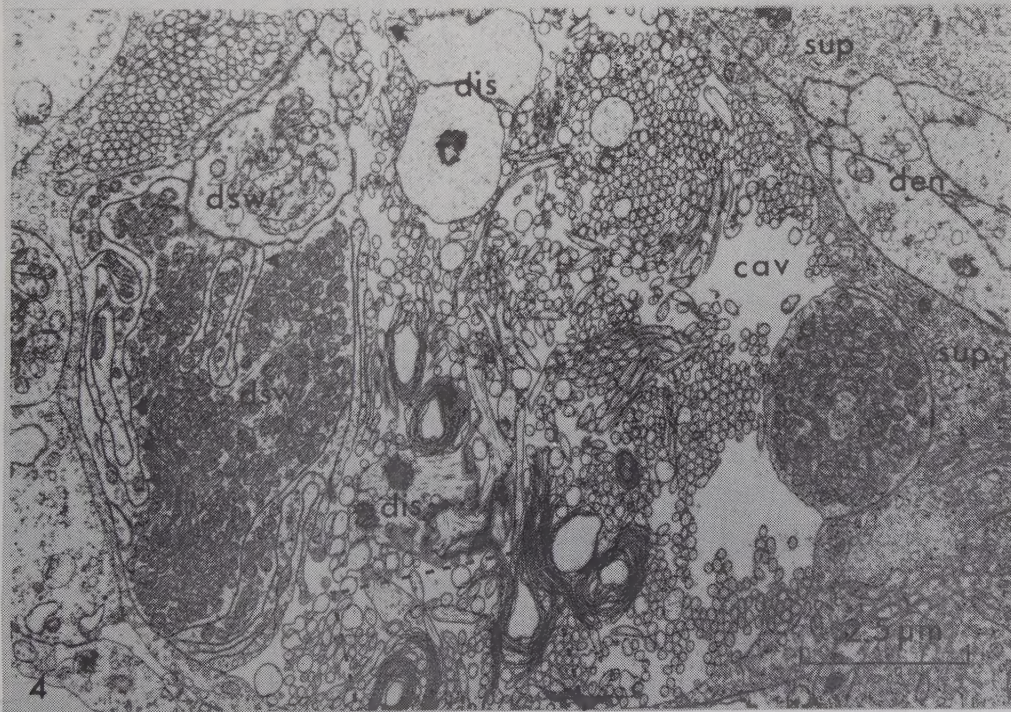
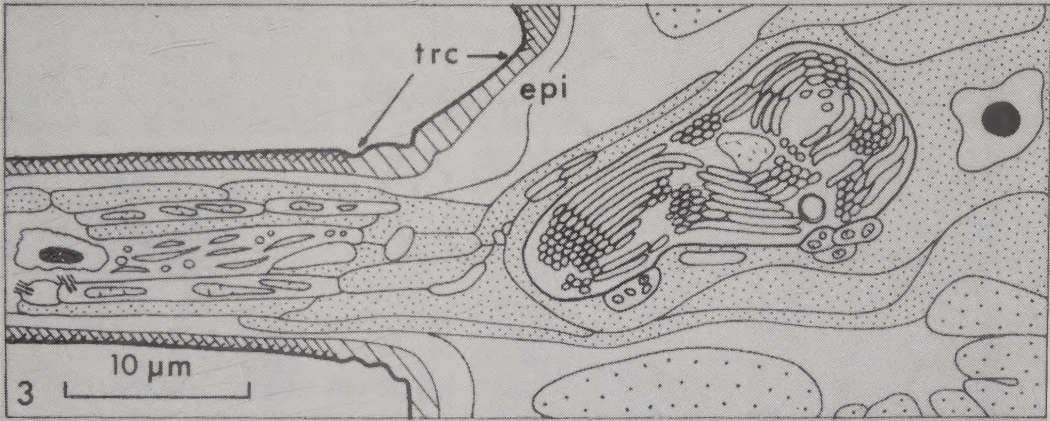
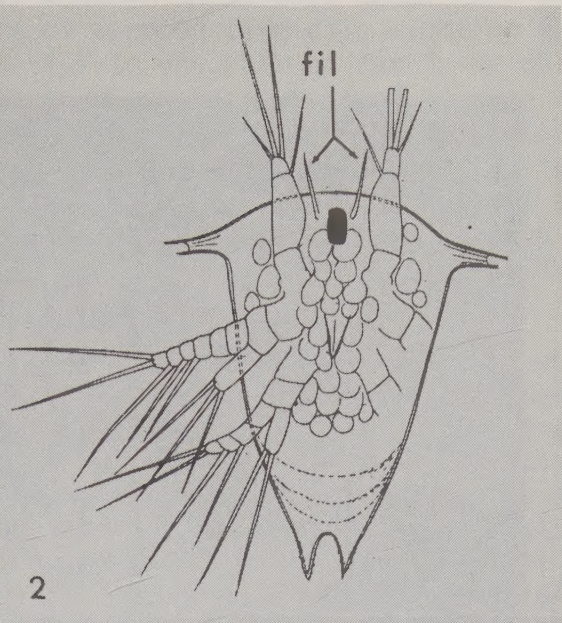
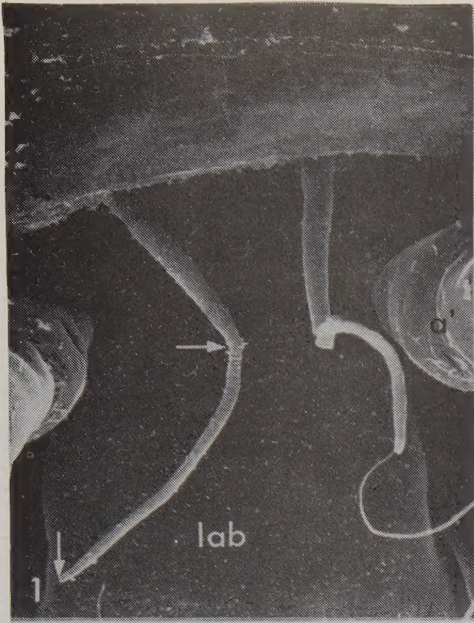
Supporting cells. Probably only two of the supporting cells border directly to the oB cavity. Often the entire wall thickness is made up by only one supporting cell process (Fig 6). The supporting cells also give support to the dendrites in the distal part of the organ complex nerve (Fig 3, 4). The cytoplasm of the supporting cells has a higher electron density in comparison with that of protocerebral neurones, and individual cells show differences in electron density. Processes from supporting cells might project into the oB cavity, partly covering the dendritic swellings (Fig 5).

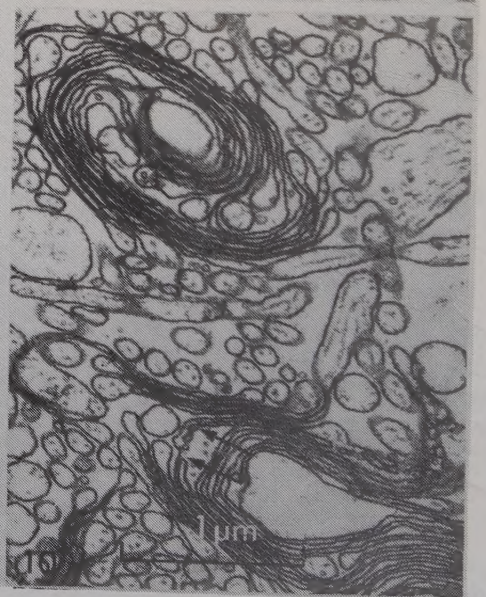
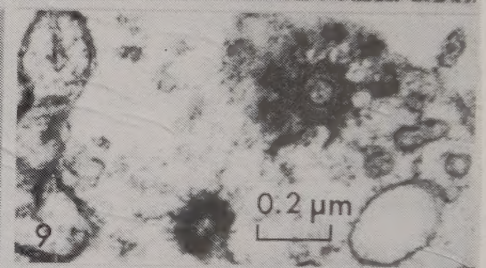
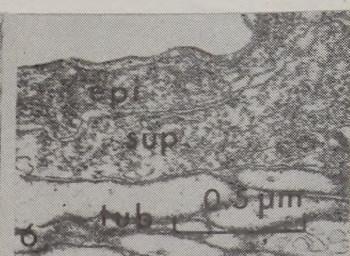
Fig 1 Anterior part of metanauplius. Below the anterior edge of the carapax the frontal filaments originate. a - antennula; arrows - distal part of the frontal filaments; lab - labrum; SEM.

Fig 2 Nauplius II of *Peltoaster sulcatus* (Cirripedia Rhizocephala) viewed from the ventral side. fil - frontal filaments; (From Nilsson-Cantell, 1921).

Fig 3 Diagram of frontal filament and oB in early moulting phase. The supporting cells are shown finely stippled and a nucleus with prominent nucleolus is seen on the extreme right. Profiles of dendrites are located between the supporting cell processes and bordering to the oB and filament cavities. In the filament, dendritic terminals with ciliary bases and one cilium of the distended type are seen along with ciliary branches from the oB. The contents of the oB cavity are shown in Fig. 4. epi - epidermal cells; trc - transitional cuticle.

Fig 4 OB in an early moulting phase. Spiralled ciliary branches are shown in lower centre. Dendritic swellings (dsw) with interdigitations between individual terminations (arrowheads). cav - organ cavity; den - dendrites; dis - pairs of ciliary distensions; sup - supporting cells; (The location of Fig 10 is indicated by broken line in lower centre. The dsw region to the right is shown in Fig 7.)





The cavity and dendrites. Terminal dendritic swellings from at least four neurones have been observed in the cavity (Fig 4). The cytoplasm of the terminals characteristically has a large number of mitochondria, which might show differences in size and density between individual dendrites. Interdigitations between the plasma membranes of apposed terminals might be formed (Fig 4). A terminal as a rule gives rise to one pair of ramifying cilia, but all dendrites observed in the cavity have not been verified to give rise to cilia. In preparations from all examined phases of the moulting cycle the ciliary ramifications appear to have a random distribution in the organ cavity, and only exceptionally the ramifications appear to be located close to the cavity walls. Only small amounts of electron dense material has been observed in the cavity, eg distally in the connection towards the filament cavity (Fig 11).

The cilia. The cilia are recognized from the basal 500 nm (Fig 8), where an axoneme of 9+0 configuration is found. The diameter of the cilium here is approximately 250 nm. A basal body of 180 nm in diameter is present and around this, electron dense structures (ca 75 nm) are observed. These structures are connected to the 9 longitudinal elements through "spokes", which have an angle with the radius. The overall diameter of the basal apparatus approximates 400 nm. The peripheral structures have not been established from all basal bodies encountered, which might indicate the presence of two types of basal bodies, but, as the peripheral structures are present along a part of the basal body only, it might also be that the peripheral structures are missed in some preparations, due to difficulties in obtaining unbroken series of sections of all basal bodies examined. Rootlets diverge from the basal bodies. The period of their transverse striation is ca 60 nm. Close to the basal body the rootlets are found in an area of cytoplasm devoid of mitochondria or other structural elements (Fig 7). This area might be circular in cross sections, but often has an irregular profile. It is more or less completely surrounded by cisternae of the reticulum (fig 7). Distally the cilium distends, measuring up to a few μm in size, the axonema loses its organization and numerous microtubules appear at a random distribution (Fig 8). The microtubules of the axonema often are observed to follow close to the membrane of the ciliary distension. Bifurcating microtubules have not been observed. Centrally in the ciliary distensions electron dense material of a granular appearance is found (Fig 4, 7).

Fig 5 OB cavity in apolysing larva. arrows - myeloid figures; open arrows - supporting cell processes; dsw - dendritic swellings; mit - microtubules; tub - tubular ciliary branches; ves - vesicular material.

Fig 6 Organ wall in VI stage larva undergoing apolysis. epi - epidermis of cypris; tub - tubular ciliary branches; sup - supporting cell.

Fig 7 Dendritic swelling with reticulum cisterns around rootlets (arrows). The organ cavity to the left. sup - supporting cell with rough endoplasmic reticulum. (Enlargement of part of a section adjacent to that shown in Fig 4).

Fig 8 OB in later phase of moulting cycle with two dendritic swellings and, on the lower right, part of a supporting cell. A pair of cilia emerges from the terminal in the centre. arrows - vesicular material; dis - distended cilium; edm - electron dense material.

Fig 9 A pair of basal bodies in cross section.

Fig 10 OB cavity in later phase of moulting cycle. Spiralled ciliary branches and vesiculation of apposed membranes, between arrows, are shown (Enlargement of area indicated in Fig 4).

Numerous microtubules emerge from this dense material or appear to pass through the material. In more peripheral parts of the distension electron-optimally empty vesicular material is interspersed with the profiles of microtubules (Fig 5). The vesicular profiles often have an irregular shape and their mean size is 140 nm with a range of 25 nm - 250 nm. The microtubules enter the ciliary branches which ramify successively until a terminal diameter of ca 100 nm is reached. Each terminal branch accepts from one to a few microtubules (Fig 5, 10). Occasionally flattened ciliary branches are spiralled into whorls of up to a few μm in size (Fig 4, 10). Also concentric arrangements of the flattened branches occur. In a few instances vesiculation of apposed membranes has been observed (Fig 10).

Changes during the moulting cycle. The modified cilia and the supporting cells show a variation in their fine structure during the moulting cycle, while the dendritic swellings appear to be unaffected.

The ciliary distensions in the premolt larva, undergoing apolysis, contain a large amount of the vesicular material, which also is found locally in the ramifications (Fig 5). The vesicles usually are absent from ramifications with diameters below 250 nm. Later during a larval stage the number of vesicles dwindles and might become nil. Also myeloid figures (Fig 5) are frequent in the early phases, being practically non-existent later on in a stage. These figures show an individual variation in size, but profiles measuring up to 1,5 μm were common in the apolysing larvae. The amount of ciliary ramifications in the cavity might be larger in moulting specimens, as less free space is observed in the cavities during early phases. This might be brought about either by an increase in the number of ramifications or by an increase in the length of individual ramifications. In the former case a certain increase in the number of microtubules in the distended part of the cilium would be expected, as at least most microtubules appear to originate in the distension.

In the early phases of a moulting cycle the cytoplasm of the supporting cells shows a greater electron density and a higher development of the endoplasmic reticulum so as to practically obliterate the remaining cytoplasmic structure. At the same time the nucleus shows an irregular outline. These changes parallel those in the epidermal cells but in those it always is possible to examine the cytoplasmic structure.

The frontal filaments

The frontal filaments lack articulations but have a proximal and a distal part (Fig 1) as also demonstrated by Walker (1974). The cuticle in a mid-stage larva measures ca 1 μm proximally, but the thickness dwindles distally in the proximal part (Fig 13, 14). In the distal part the cuticle measures inside a few hundred nm in early larvae (Fig 18). The thicker cuticle in the proximal part is reflected in the greater rigidity of this region compared to that of the distal part (Fig 1). The distal thin cuticle also is indicated by the folds that appear locally. Basally, where the frontal filament attaches to the larval body, the cuticle is less electron dense and appears thicker with a less compact organization of the fibrillar laminae (Fig 13). This characteristic of the attachment region is lost peripherally, where the cuticle recovers the more compact, electrondense configuration.

Cellular material to the filament is contributed by the epidermal cells proximal to the filament origin, the supporting cells found around the oB, the dendrites originating in the protocerebrum and the ciliary ramifications which reach into the filament from the oB.

The epidermal cell processes form a continuous layer in the range of 500 nm in moulting and early phase larvae (Fig 11, 12). Before the actual moult the external plasma membrane of the epidermal cell processes is folded, as a preformation for subsequent growth (Fig 12). Later in each stage the epidermal processes are more or less withdrawn from the filament, partly uncovering the internal surface of the cuticle (Fig 18). This is reflected also in the apparently larger space of the extracellular cavity. In preparation of the next moult the epidermal layer is reestablished.

The processes from the supporting cells in the basal part of a filament are arranged into two layers. The central layer is continuous with the bordering layer of the oB cavity and envelopes the narrow space containing the ciliary branches from the oB. This space also connects the oB cavity with that of the filament. External to this layer, and bordering to the epidermal cells peripherally, are processes from another supporting cell, often of slightly lower cytoplasmic density. Between them these supporting cell layers contain the some 15 dendrites entering the filament (Fig 11). The dendrites in this basal region are entirely isolated from one another by the supporting cells, either included between two cell processes or wrapped in one of the cells. In the latter case a mesaxone is formed (Fig 11). This arrangement contrasts with that found proximally in the nerve, where the dendrites might be apposed to one another (Fig 4). Apposition of dendrites also occurs in the filament, where the supporting cells terminate (Fig 17).

The dendrites terminate in the proximal part of the filament and the two types of cilia (Walker, 1974) which arise from the dendrites, are recognized (Fig 17). The mitochondria of the filament dendrites are less numerous, have an elongated shape and are distributed along a greater length of the dendrite than those of the oB dendritic terminals.

The club shaped cilium, reminiscent of the oB cilia but for its shorter and less uniform branches, has a conspicuous amount of electron dense material in the distended part of the shaft.

The second, slender type of cilium arises singly from a dendrite and lacks this dense material. The basal apparatus of the slender cilia is characterized by a basal body ca 150 nm in diameter, rootlets of 55 - 60 nm striation period, and a centriole (150 nm in diameter) located 150 nm below the basal body under right angles to the cilium-rootlet axis (Fig 15). The cilia have a neck region 0,5 - 1 μ m long. Along the neck accessory electron dense material is associated with the axonemal structures (Fig 12, 16, 17). Part of this material is located between the axoneme and the ciliary membrane. This peripheral dense material in some of the slender cilia might extend also distal to the neck (Fig 12, arrow). Within this region the ciliary diameter is uniformly ca 200 nm (Fig 16) and the axonemal structure (9+0) apparently is intact to be lost further distally.

A total of 14 slender cilia have been recorded in the filament. Along the shaft the slender cilia locally have bulbous distensions. In these places the ciliary diameter might be doubled and, apart from microtubules, also contents of vesicular material and myeloid figures might be found. Along the ciliary membrane extraciliary dense material is present, which might bridge gaps of at least 65 nm between individual shafts. Clear junctional contacts between individual shafts and between shafts and epidermal cell processes are not found, but locally membranes might be tightly apposed resulting in a denser area that cannot be examined further.

In the distal part of the filament (Fig 18), the cilia are found along with epidermal cell processes in the cavity. The ciliary profiles here are irregular with a random distribution of the microtubules. Also the diameter of the ciliary profiles varies. The number of profiles does not indicate a ramification of the cilia. The epidermal cell processes are slightly denser electronoptically, as compared to the cilia. Small processes from the epidermal cells make contact with the cuticle.

Fig 11 Frontal filament in early moulting phase. Transverse section of filament basally. arrows - mesaxons; circle - electron dense material in cavity; cut - cuticle; den - dendrites; epi - epidermis; tub - tubular ciliary branches from oB; sup - supporting cells.

Fig 12 Frontal filament in apolysing larva. Longitudinal section of proximal part. Epidermal cells with new cuticle (epi) and external folds on lower right. arrows - electron dense material associated with the axoneme; bbo - basal body with rootlets; cen - centrioles; sup - supporting cell.

Fig 13 Frontal filament in later phase of moulting cycle. The epidermal processes are receding. The transitional cuticle is seen in lower part of figure.

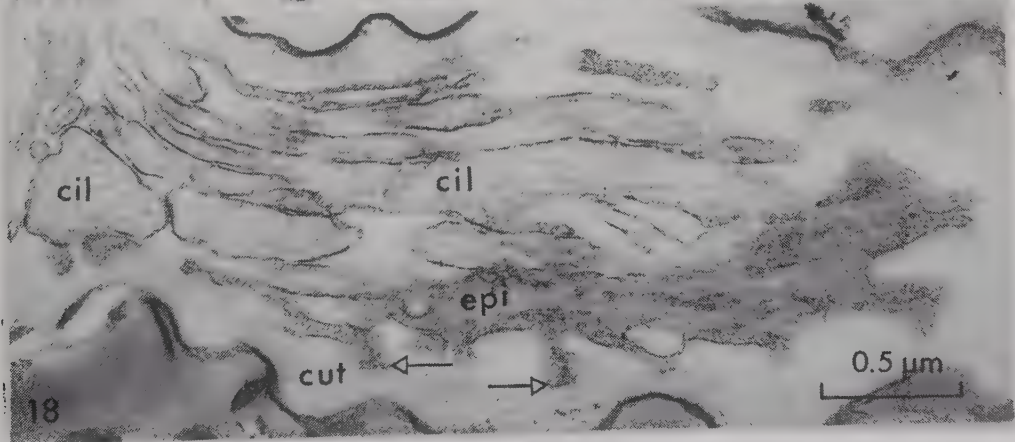
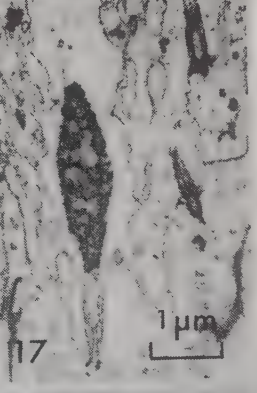
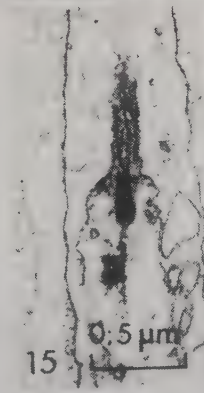
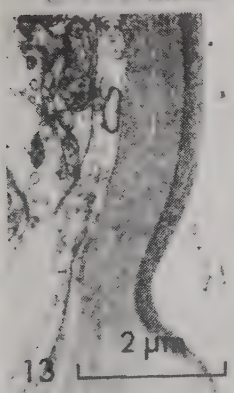
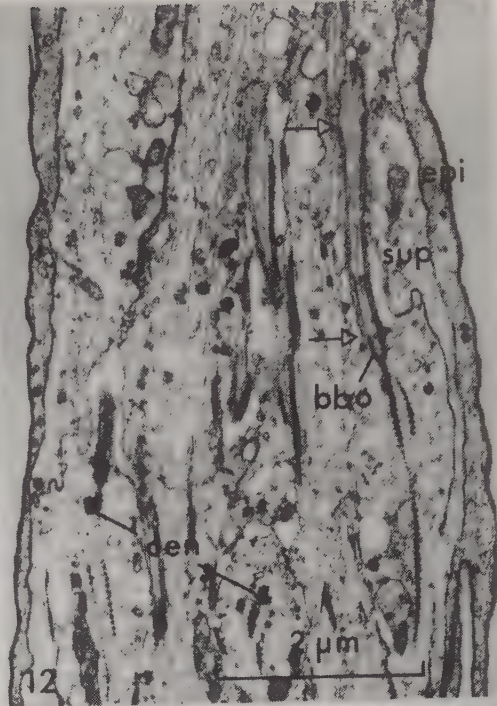
Fig 14 Frontal filament in later phase of moulting cycle. Proximal part of filament distally. Note the absence of epidermis.

Fig 15 Frontal filament in later phase of moulting cycle. Terminating dendrite with single cilium. The centriole is located proximal to the basal body and at right angles to the cilium - rootlet axis.

Fig 16 Frontal filament in later phase of moulting cycle with electron dense material associated with axoneme basally in cilium (arrows).

Fig 17 Frontal filament in later phase of moulting cycle with club shaped, distended cilium with contents of electron dense material. To the right two apposed terminating dendrites are shown.

Fig 18 Frontal filament in early moulting phase with ciliary shafts distally (cil). Epidermal cell profiles (epi) in contact with cuticle (arrows). cut - cuticle.



The frontal filament - organ of Bellonci complex in Cirripedia Thoracica

The present examination of the frontal filament-oB complex in the thoracican nauplius agrees well with that given by Walker (1974). A number of minor individual characteristics such as the number of supporting cells around the oB and of the dendrites and cilia in the oB and the filament might be explained as interspecies variations or also as variations between different larval stages.

Other points where the examinations do not agree are more difficult to explain. The question of possible bifurcations in the microtubules is one. It is agreed that the region in the distended cilia where bifurcations would be expected is difficult to examine due to the accumulation of electron dense material. Nevertheless the character of the microtubules, which can be seen clearly, rather indicates an absence of bifurcations. Moreover the axonemal tubules often are observed to follow the distending ciliary membrane, which apparently brings them to a position at a distance from the most probable region of bifurcation. A de novo formation of microtubules in the cilium appears to be the case. Absence of bifurcation in microtubules also is more generally accepted (Nadelhaft, 1974; Ha, 1970). Also the occurrence of small basal bodies (60 nm in diameter; Walker, loc cit) is incompatible with observations in B. improvisus, where basal bodies usually measure 150 nm - 200 nm in diameter.

The latter figures compare more favorably with the generally accepted dimensions (Pitelka in Sleight, 1974).

The importance of accounting for changes during the moulting cycle is borne out by what is shown here for the behaviour of the epidermal cells in the filament area. First the uninterrupted epidermal layer in moulting specimens might impose functional problems regarding the filament receptors, especially in discussing a chemoreceptory function. A second question involves the probable communication between the filament cavity and the subepidermal spaces in intermoult specimens where the epidermal cell processes are more or less withdrawn from the filament leaving a space free to diffusion between the cuticle and the supporting cell processes. This condition however is rather hypothetical as the preparations might show osmotically derived artefacts. The situation shown in Fig 13 moreover is characteristic to the intermoult between nauplius VI and the cypris, where the new cuticle will be formed along the oB, and might not be representative for intermoult between individual nauplius stages.

The changes in the modified cilia and the supporting cells of the oB during the moulting cycle indicate a functional relationship between individual elements of the oB and a relation of the oB to the cycle. This is discussed more fully in the context of oB function among the Crustacea generally (Kauri; MS).

The supply of dendrites to the organ complex shows a point of interest. The dendrites are protected by the supporting cells except in the terminal areas. The individual dendrites as a rule are apposed to each other while bypassing the oB and also subterminally within the filament, but in the basal part of the filament each dendrite is isolated individually. The only apparent characteristic of this region is that it is the region where the basal part of the filament bends relative to the larval body, the transitional cuticle of this region (Fig 13) apparently being flexible. The observed isolation of the dendrites then would protect the dendrites from mechanical stress.

The two types of cilia in the filament might indicate a dual function (Walker, loc cit). The ramified cilia are reminiscent of the oB cilia except for their less uniform diameter and lack of aggregation into bundles. The simple cilia are unique in that only a single cilium emerges from each slender dendrite. The basal apparatus with an accessory centriole also is a characteristic of this type of cilium.

The interrelations between individual ciliary shafts and between these and epidermal cell processes are interesting from a functional point of view, especially considering a mechanoreceptory function. The adhesion between shafts and hypodermis (Walker, loc cit) might involve the dense material, reported in the present examination. Though no clear junctional structures have been observed in this area in *B. improvisus*, the proximal parts of cilia might be sufficiently bound mechanically to be exposed to forces of shear when the filaments bend. Distally the shafts apparently are suspended individually in the filament cavity.

The communication between the filament and the oB cavities is peculiar to the barnacle larvae. The significance of this for the function and homology of the organ complex is discussed together with other cephalic organs among the Maxillopoda.

The organ of Bellonci in Derocheilocaris remanei

The anterior part of the head. Anteriorly the head in *D. remanei* has a pair of lobes, which carry a pair of setae distally (Fig. 19). In these lobes the anterior parts of the oB are located. The posterior parts of the organs are tightly apposed to each other medially, posterior to the head lobes. Only one cavity is present in the oB but this is nearly separated into anterior and posterior parts by a partition ventrally (Fig. 19 B, 20, 21). Cellular elements are contributed to the organ by supporting cells and from the anterior part of the protocerebrum, by sensory neurones.

Close to the bases of the distal setae ciliary structures are found, indicating a sensory function of the setae, but no connection could be found between the setal arrangement and the oB.

The surface of the oB shows no major specializations, except in the nerve area. Over part of its surface the organ is in contact with the epidermis, partly it borders to the haemocoel, and posteriorly, to the protocerebrum.

The cavity. In the cavity of the organ intensely electron dense bodies a few μm across are located (Fig. 21). These bodies have an irregular outline. Frequently the bodies are found in a central position in both parts of the organ.

There is a surprisingly good bilateral agreement of the individual components in the organ cavities (Fig. 20).

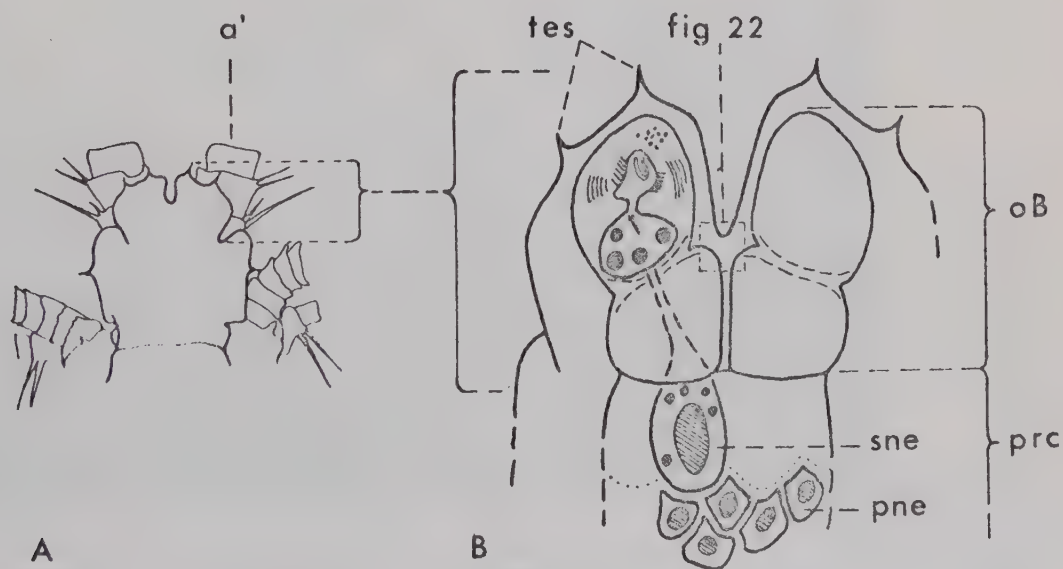


Fig. 19 A. Head region of *Derocheilocaris remanei* (After Chappuis and Delamare Deboutteville, 1954). B. OB and anterior part of protocerebrum. $\hat{a}$ - antennula; oB - organ of Bellonci with the separation between anterior and posterior parts indicated; pne - protocerebral neurone; prc - protocerebrum; sne - sensory neurone; The location of the section in Fig. 22 is indicated in B.

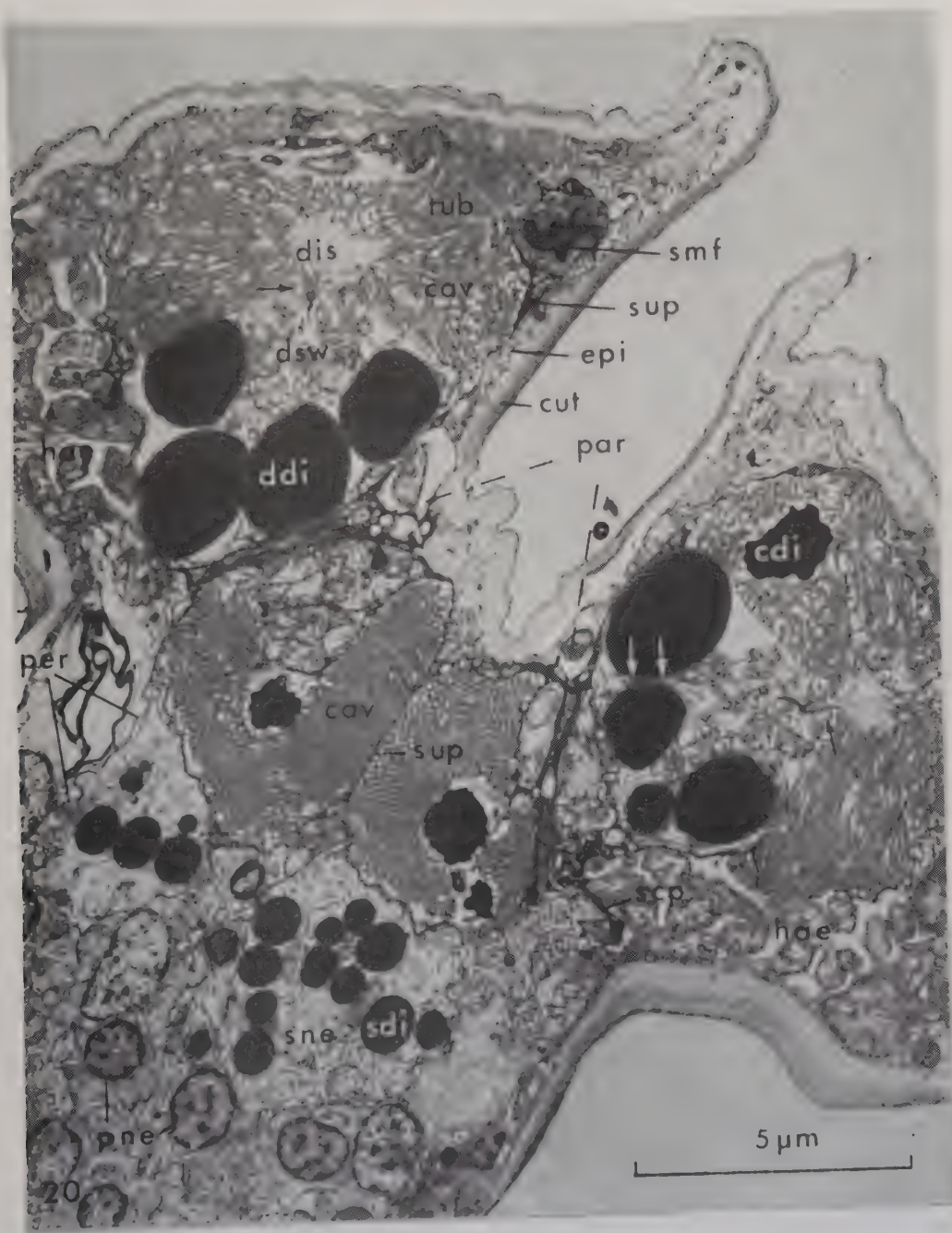
The supporting cells. The cavity wall is built up of thin processes from supporting cells (Fig. 20, 21, 22). At least two supporting cells partake in the formation of the organ. One cell is located in the ventral region of the anterior part of the organ and one is found anteriorly in the posterior part of the organ, close to the median plane.

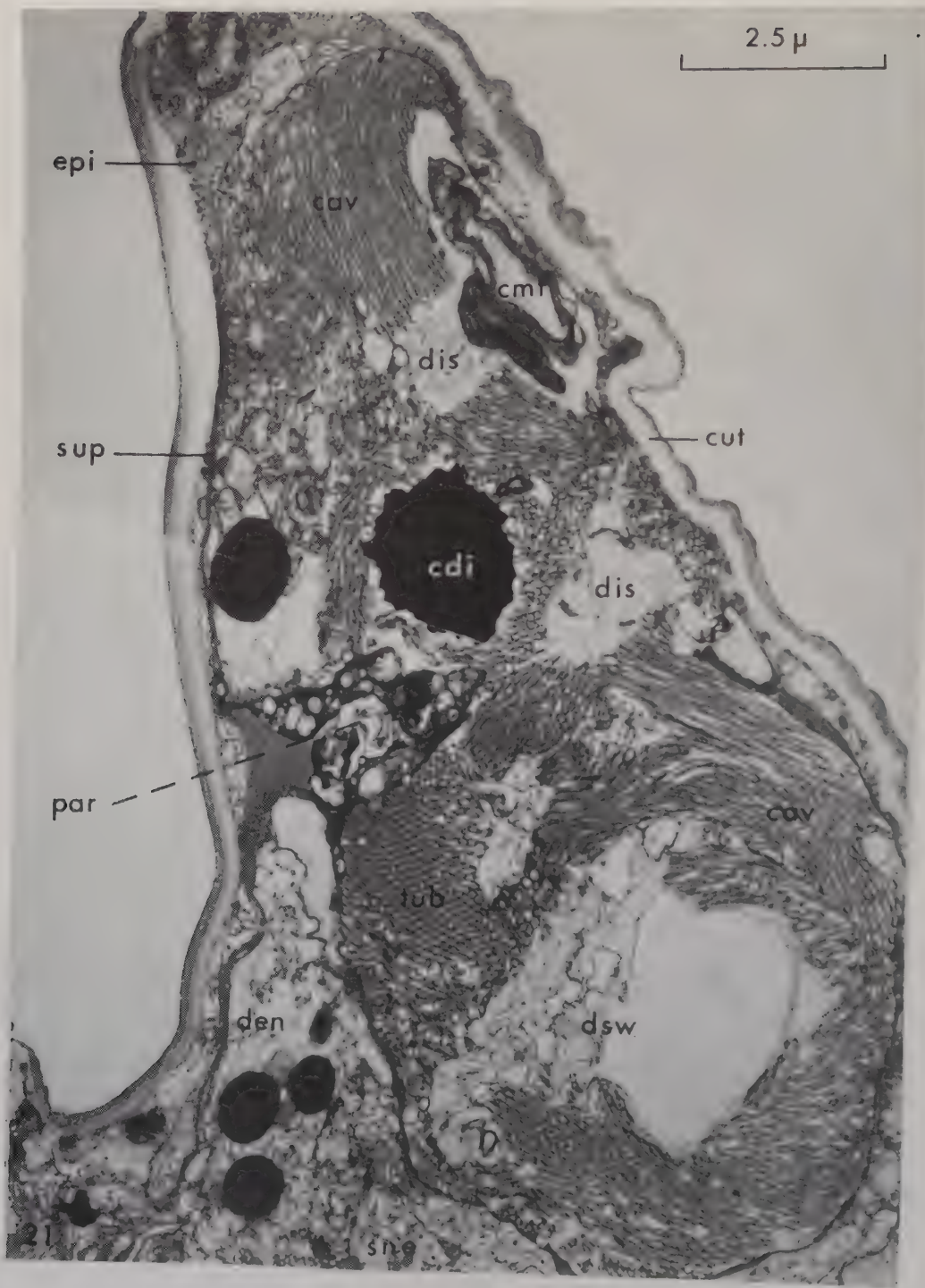
Especially the cells in the posterior part have small, flattened nuclei (Fig. 22), while those of the anterior part have nuclei of a more spherical shape. Both the nuclei and the cytoplasm have a high electron density when compared to that of the epidermal cells or that of the protocerebral neurone perikarya. The flattened cell processes range from 20 nm to 100 nm in thickness over most of the organ surface, but larger thickness occurs in the perikarya and in local distensions. The latter might approach a μm or more. In the distensions the cytoplasm contains vacuoles of varying size (Fig. 21, 22), which contain what appears to be fragments of membranes or tubules, reminiscent of the tubular branches in the cavity. Also myeloid figures are observed (Fig. 20), but no endoplasmic reticulum or mitochondria. These structures might be obscured by the high electron density, but even so there is a very small amount of cytoplasm left, both in the extremely thin processes and in the distended parts which mainly contain the nucleus or the vacuoles. The supporting cells take part in the formation of the ventral partition in the cavity (Fig. 20, 21). Processes from the supporting cells project into both the organ cavity and into the haemocoel around the organ (Fig. 20).

The protocerebrum. Anteriorly in the protocerebrum two different neurone types are found (Fig. 20). The larger, sensory, neurones and the smaller, generally occurring protocerebral neurones. The latter have a size ca $1,5 \mu\text{m}$ by $2,5 \mu\text{m}$ and a slightly elongated nucleus $> 1,5 \mu\text{m}$ in length. These neurones have not been more closely examined. The profiles of the sensory neurones are ca twice this size and have a nucleus ca $2,5 \mu\text{m}$ long. (The size estimates of especially the sensory neurones are uncertain due to the small number of profiles in the sectioned material.) The cytoplasm and nucleus of the sensory neurones are less electron dense in comparison with those of the smaller neurone type.

The protocerebrum is covered by a thin layer of perilemmal cells. This layer is formed by cell processes similar to those of the supporting cells in dimensions, but without the vacuolized areas, characteristic of the supporting cells (Fig. 20). Processes from the perilemmal cells are given off into the protocerebrum between the neurone perikarya. The perilemmal and supporting cell processes are apposed in the region where the oB comes in close contact with the anterior margin of the protocerebrum (Fig. 20, 21).

Fig. 20 Horizontal section through the oB and protocerebrum in anterior part of the head. The supporting cells (sup) with processes into the haemocoel (scp) and myeloid figures (smf); the sensory neurones (sne) with dense inclusions (sdi); the dendritic swellings (dsw) with dense inclusions (ddi) and dense material close to these (white arrows); the cilia (black arrows) with distensions (dis) and tubular branches (tub); the organ cavity (cav) with dense inclusion (cdi); the haemocoel with haemocytes (hae); cut - cuticle; epi - epidermis; par - ventral partitions; per - perilemmal cells; pne - neurone perikaryon in protocerebrum.





The sensory neurones. The sensory neurones are situated beneath the proto-cerebral perilemma anteriorly (Fig. 20). Their dendrites reach the ventral side of the oB (Fig. 21), and penetrate the supporting cells in the ventral partition. Inside the cavity the dendrites distend to terminal swellings, carrying cilia (Fig. 20). Apparently the anterior and posterior parts of the organ are entered by two dendrites each. The axons have not been examined here, but probably leave the perikarya in a postero-ventral direction.

Characteristically the cytoplasm of the perikarya contains several large osmiophilic inclusions of varying size ($< 1 \mu\text{m}$). Short lengths of membrane along the inclusions are interpreted as narrow profiles of smooth endoplasmic reticulum, but might represent a limiting membrane. The inclusions are distributed throughout the perikaryon, and also are found in the basal parts of the dendrite (Fig. 20, 21). Occasional mitochondria and endoplasmic reticulum of the smooth and rough types are present. The reticulum cisterns often have a swollen appearance. Areas devoid of cytoplasmic structure, other than diffuse electron dense material, are interpreted as indications of storage of material which might have been eluted during processing. These areas are $1 \mu\text{m} - 2 \mu\text{m}$ across.

The dendrites. Short dendrites connect the neurone perikarya to the terminal dendritic swellings (Fig. 20). The latter range from a few μm to a size comparable to that of the perikaryon (ca $5 \mu\text{m}$). In the periphery of these swellings large osmiophilic inclusions ($< 2,5 \mu\text{m}$) and an area where cilia originate, are found. The central part of the swelling and the ciliary area have a large population of mitochondria, while close to the inclusions there are large cisterns of the smooth endoplasmic reticulum. Here also locally small aggregations of dense material are found (Fig. 20, white arrows). In sections treated with lead citrate, staining is obtained in this material. The apposed cisterns might be distended, probably due to osmotic processes during the preparation of the material. This might indicate a high content of metabolites. The cisterns and the inclusions are situated close to the dendritic plasma membrane. The inclusions, except their larger size, have the same appearance in the dendritic terminals as in the perikarya. Vesicular material is rarely found in the dendritic terminals.

The cilia. Two cilia arise from each dendrite (Fig. 23). A short neck region (diam.: 250 nm , length: $\leq 500 \text{ nm}$) rapidly distends into a ciliary shaft of irregular shape, which might approach the terminal swelling in size (Fig. 20, 24). Only the neck region contains an axoneme with the longitudinal elements arranged in a 9+0 pattern. At the base of the axoneme a basal body is found.

Fig. 21 Longitudinal section in a vertical plane through the oB.
 cav - organ cavity; cdi - dense inclusion in cavity; cmf - ciliary myeloid figure; cut - cuticle; den - dendrite; dis - ciliary distension; dsw - dendritic swelling with distended cistern; epi - epidermis; par - ventral partition; sne - sensory neurone; sup - supporting cell; tub - tubular branches.

The basal bodies are distinguished from the ciliary axoneme through their higher electron density (Fig. 24). Electron dense material also is present in the transitional region (Fig. 23, 24) but distinct basal plates or transitional fibres are not formed. The rootlets originate from the proximal part of the basal bodies. Characteristically the rootlets take an oblique direction to the longitudinal axis emerging from the place of origin, which lies on the internal side of the tubular elements of the basal body (Fig. 23). A transverse striation with a period of 55 nm is present and the rootlets split shortly after their origin. In the ciliary neck region dense material connects the axonemal elements with the ciliary membrane (Fig. 23). The neck region might be drawn into the dendrite, in which case a circumciliary space is formed. In the distended part of the cilium the axonemal organisation is lost and a large number of microtubuli (diam.: 22 nm) with their axes in a random arrangement appears (Fig. 24, 25). From the ciliary membrane a large number of tubular branches is formed. Close to the place of origin there is a constriction (Fig. 24, 25) where the tubule diameter approximates 70 nm, but only 100 nm from the shaft surface the diameter has increased to ca 100 nm. The diameter then is unchanged throughout the branches with the exception of occasional distensions distally (Fig. 24). The branches do not ramify. Generally each of these branches is entered by one microtubule from the distended ciliary shaft but profiles with two or three microtubules occur. Electron dense material frequently is present in the distended cilia. It takes the shape of myeloid figures with more or less distinctly defined membrane structure (Fig. 21). These formations usually occur randomly, but sometimes are arranged parallel to the ciliary surface, beneath the origin of the tubular branches.

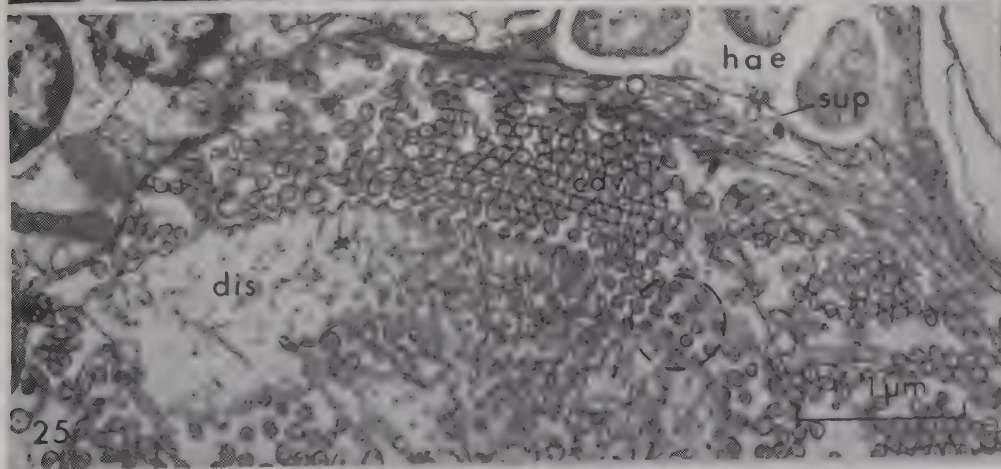
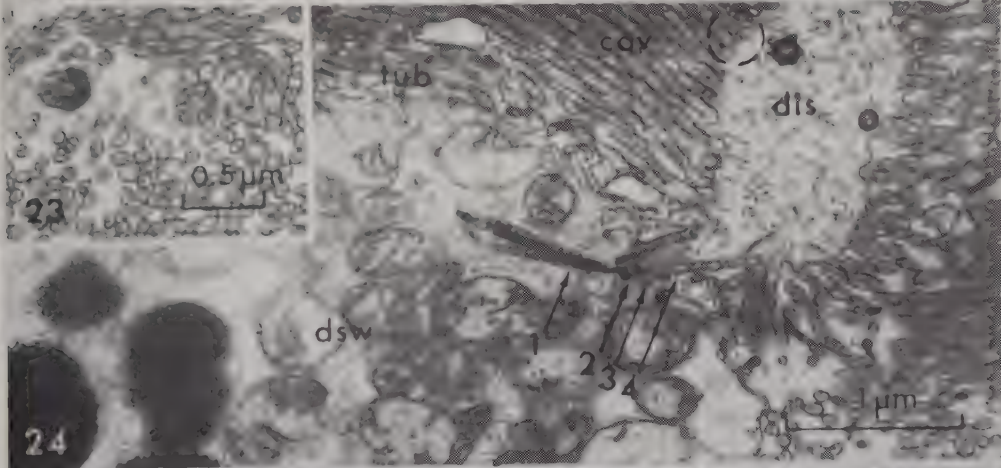
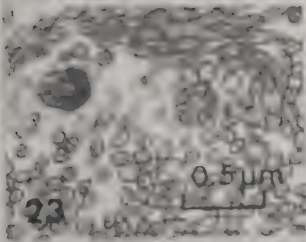
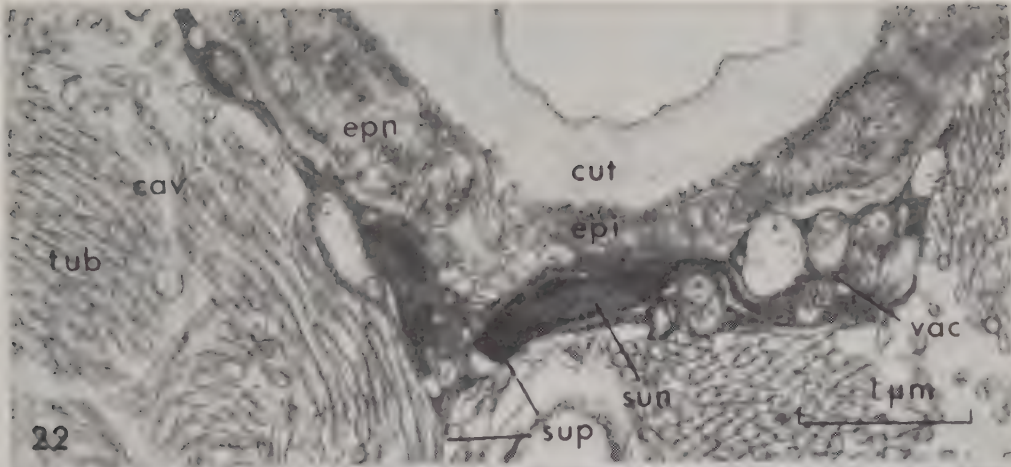
The haemocoel. Around the organ the haemocoel is best developed around the postero-lateral (Fig. 20) and ventral parts. Smaller spaces, which also reach positions distally along the organ, measure about $0,6\ \mu\text{m}$. The organ surface borders directly to the haemocoel, without the formation of an intermediate basal lamella. The profiles of the haemocytes vary in shape and size but average $0,6\ \mu\text{m}$ by $1,2\ \mu\text{m}$, the larger ones measuring $0,6\ \mu\text{m}$ by $1,9\ \mu\text{m}$.

Fig. 22 Horizontal section through posterior parts of both oB. Epidermal cell (epi) with nucleus (epn); supporting cells (sup) in the median plane with nucleus (sun) and vacuolated cytoplasm (vac); cav - organ cavity; cut - cuticles; tub - tubular branches. (Approximate position of section is indicated in Fig. 1)

Fig. 23 A pair of cilia in transverse section. The transitional region to the left and the neck region to the right.

Fig. 24 A section through a dendritic swelling (dsw) with dense inclusions to the left and a cilium; the arrows: 1 - rootlet; 2 - basal body; 3 - transitional region; 4 - neck region; dis - distended ciliary shaft; tub - tubular branches with distensions distally; in the broken circle the constricted proximal parts of the tubular branches are seen.

Fig. 25 A section through a ciliary distension (dis), close to the supporting cell (sup); microtubules entering the tubular branches (x) and the constricted basal region of the branches in transverse section (broken circle); organ cavity with tubular branches (cav); haemocoel with haemocytes (hae).



The organ of Bellonci in Mystacocarida

The findings on the topography of the head in D. remanei from the present examination verify the general observations given for D. typicus (Pennak and Zinn, 1943), Ctenocheilocaris galvarini (Dahl, 1952) and D. remanei (Delamare Deboutteville and Chappuis, 1954; Cals, Delamare Deboutteville and Renaud-Mornant 1971; Baccari and Renaud-Mornant, 1974).

The oB clearly is identical with the organ A as described by Baccari and Renaud-Mornant (1974). Here the two anterior lobes of organ A correspond to the anterior parts of the oB and the basal lobe in organ A to the two posterior parts of the oB.

Apparently the two pairs of eye spots in D. typicus (Pennak and Zinn, 1943) eyes in D. remanei (Delamare Deboutteville and Chappuis, 1954), are located in positions corresponding to that of the anterior and posterior parts of the oB as described here. The eyes and the oB parts are distributed with one pair of larger units anteriorly and laterally, and one pair of smaller units more posteriorly and closer to the median plane. The dark material observed might correspond to the electron dense inclusions in the cavity of the organ and the two pairs of lenses (Dahl, 1952) might be represented by aggregations of the tubular ciliary branches or by the entire oB parts. The individual differences in location of the lenses or eyes, as reported by the earlier authors, might arise through individual dislocations of the component parts, viz the aggregations of tubular branches and the central inclusions, between individual specimens. Individual variations in the inclusion numbers might explain the variations in the number of eyes, reported earlier.

The sensory neurones are included in the protocerebrum in the present description, as the natural demarcation of the protocerebrum lies along the intervening haemocolic spaces and the relatively sharp line involving the supporting cells and the perilemmal cells posterior to the oB. It might be argued that also the oB should be regarded as part of the protocerebrum, as the supporting cells and the perilemmal cells locally appear to form a continuous layer along both organs (Fig. 20). However, in the head of D. remanei this question must be taken as one of secondary importance, as the small size of the animal has brought about specializations in order to save space and cells. The close apposition of the oB on the protocerebrum must be regarded against this background. Moreover, the oB is exposed to the haemocoel and also is located close to the epidermis, why its localization functionally is a peripheral one.

The two large nerves to the oB (Baccari and Renaud-Mornant, 1974) have not been observed in the present examination, but might represent the axons from the sensory neurones.

Characteristics obtained on the fine structure reveal rather an ordinary oB as regards the component elements. However, the supporting cells, the cavity regions and the dendritic terminals with the characteristic cilia show a somewhat surprising constancy in the bilateral arrangement as seen from Fig. 20. The distended cilia, with their branches formed directly, without subsequent ramifications, are reminiscent of those in Sphaeroma serratum (Chaigneau, 1971). The two species also share the apparent lack of electron dense granular material centrally in the distended part of the cilia. The myeloid figures found in the ciliary distensions of D. remanei probably represent artefacts caused by the fixation procedure. These structures occasionally have large dimensions and then also the ciliary membrane is further distended. Both characteristics probably indicate higher contents of metabolites.

The structural observations in D. remanei indicate a few possible functional interrelationships between the individual organ elements.

These aspects are best discussed from the smallest functional unit of the organ, which appears to be either one of the organ parts. Each of these comprises supporting cells, sensory terminals and part of the cavity with a small number of the dense inclusions. The supporting cells with the dense and vacuolated cytoplasm give an impression of active cells, with a high content of electron dense metabolites. As the endoplasmic reticulum and golgi bodies are practically nonexistent, the secretory powers of the cells probably are small. This leaves, apart from delimiting and protecting the organ cavity, two probable functions: phagocytosis and mediation of metabolites in either direction. Phagocytosis might involve removal of cavity contents such as aged ciliary membranes. This is indicated by the contents of some of the vacuoles, where membranous material has been identified. The myeloid figures in the supporting cell cytoplasm might represent later stages in decomposition. Ultrastructural characteristics, similar to those found here in the supporting cells, are described from numerous phagocytizing cells such as macrophages (Hauw et al, 1975) phagocytic blood cells, and certain glia cells. An interesting phagocytosis is performed by the cells of the pigment epithelium in the vertebrate eye where aged parts of the outer segments of photoreceptor cells are ingested (Young and Bok, 1969). The processes into the organ cavity might be involved in the phagocytic mechanism.

The internal medium of the cavity should be expected to have special chemical qualities regarding the receptor membranes in order to maintain functional conditions. Unfortunately the high electron density of the cytoplasm has made it impossible to examine the intercellular spaces between apposed supporting cells for junctional complexes, which might indicate the possibilities for diffusion between cavity and haemocoel. The increase of surface provided by the supporting cell processes is interpreted as a basis for exchange between the cells and the internal and external spaces. The dendritic swellings are the only other element in contact with the cavity liquor and the dense inclusions in these dendrites are a potential store of material that might be released to the cavity. The position close to the cell membrane is a further indication of possible release. Release of electronoptically similar material from sensory neurones into the oB cavity is described from Sphaeroma serratum (Chaigneau, 1971). Whereas in Sphaeroma the release was thought to be a holocrine process, in D. remanei the process might be mero- or apocrine. In this species also a transport mechanism between perikaryon and the dendritic termination is required. Such a mechanism would have to involve a degradation of the dense material in the perikaryon in order to pass through the dendrites. The finely granular material found in association with the dense inclusions in the terminals might indicate such a transitory degradation. The structural description given here can merely indicate a possibility of transport and release, but it strongly indicates similarities in function between the two species.

The size relationships in the oB on the organ, cell and organelle levels show interesting differences. Characteristical to the head region appears to be a need to economize with space and this obviously reflects the interstitial habitat of the species, which favours a small cross section rather than a limitation of the overall length. As apparent from descriptions given by earlier authors, though not always explicitly stated, the need for space economy has a more pronounced effect on certain organ systems, while others are more slightly affected. This results in some organ systems having a proportionally larger size in comparison with other, larger species. This is exemplified by eg the nervous system in C. galvarini (Dahl, 1952).

In the oB of D. remanei the individual levels of organization are affected differently. A comparison of the individual elements to those in barnacle larvae might illustrate this. Both organisms have approximately the same length, but the barnacle larvae have a larger width by a factor of ca 6, reflecting a different set of factors determining size and shape in planktonic forms. The elongated oB in both forms approaches 20 μ m in length, indicating an appreciably larger relative size of the mystacocaridean organ. Differences on the cellular level are found in sensory neurone and supporting cell dimensions. The size of the sensory neurone nuclei in Balanus (Kauri, 1962, and unpublished) are larger by a factor of ca 3. This approximately reflects also the size relation between the perikarya. The relative size of supporting cells is more difficult to estimate, but in D. remanei the processes of these cells are extremely thin (down to 20 nm) over large areas of the organ surface, while those in Balanus generally have larger dimensions. Similar relations are found between protocerebral neurone perikarya of the two genera, as indicated by the diameter of the nuclei, which in Balanus are larger by a factor of ca 4. The dimensions of individual parts of the neurones inside the cavities and of the organelles are almost identical in size in both forms. This is evident for the dendritic terminals, basal bodies, ciliary distensions and for the ciliary ramifications. Thus the oB in Derocheilocaris as compared to that in Balanus is relatively larger while the relative dimensions on the cellular level are smaller.

A few speculations relating to these relationships might be allowed. Assuming that the mechanisms of sensory reception in the oB are located to the enlarged ciliary membranes, a minimum surface of these membranes, which satisfies the functional demands in any one species, might be conceived. This indirectly determines the size of the organ, which obviously has a lower limit. Below this limit proper function cannot be maintained. On the cellular level space apparently has been saved by a reduction of the amount of endoplasmic reticulum in the supporting cells. The synthetic capacity, as indicated by the presence of endoplasmic reticulum in these cells in other species, obviously will have to be replaced by a supply of metabolites from other sources. Ultrastructural characteristics which might give a clue to the causes of small size, observed in the sensory neurones, have not been found. The perikarya have an ultrastructure similar to that found in other oB, excepting the characteristical dense inclusions (cf Chaigneau, 1971; Kauri and Dahl, 1975).

The size of the dendritic swellings is not affected. Their size is partly brought about by their contents of mitochondria and similar concentrations of mitochondria are found in the dendritic terminals of the oB in other crustaceans, where relatively long dendrites occur. Apart from the oB in *Balanus*, this is observed in eg calanoid copepods (Elofsson, 1971), *Doropygus* (Dudley, 1972), *Anaspides* (Kauri and Lake, 1972) and *Boreomysis* (Kauri and Dahl, 1975). In species with shorter dendrites, the mitochondria might be less numerous, as in eg *Diastylis* (Kauri, MS 2). Finally the agreement in size, observed in the ciliary structures, is expected for an oB with the tubular type of ramification in its cilia. The dimensions observed agree with what is either found generally for cilia or is found to be a common size for elements in the oB from different species (Chaigneau, 1971, 1972; Elofsson, 1971; Dudley, 1972; Kauri and Lake, 1972; Kauri and Dahl, 1974; Dahl and Kauri, MS) and should reflect nearly optimal dimensions for the receptory processes on the molecular level in these receptors.

The organ of Bellonci complex in Maxillopoda

The elements of the oB complex in the Maxillopoda are characterized by their location anteriorly in the head and by their innervation through a common nerve from the medulla terminalis or a corresponding part of the protocerebrum.

The most complex organization is found in the Copepoda, where the calanoid copepods have three different receptors (= units, Elofsson, 1971). Of the first of these only the nerve is described along a part of its length. The distal terminations are located to a pair of setae in the front. It is difficult to discuss this receptor further until more is known about its structure and proximal connections. The only possible candidates with a comparable location are the anterior setae of the Mystacocarida. As demonstrated in *Ctenocheilocaris* (Dahl, 1952), the innervation of these might derive from a region which would lie posterior to the oB neurones as shown in the present examination, why a connection might be conceivable within the protocerebrum. The second, deep receptor comprises a closed cavity below the integument with individual differences in position between species. The third, superficial receptor, finally is found apposed to the integument, which makes up the distal wall of the cavity of this organ.

The organ complex in the notodelphyid copepods (Dudley, 1972) comprises two end organs. The end organ A has a cavity enclosed in a single supporting cell, deeper in the head, while the end organ B is located as the superficial receptor above, apposed to the integument.

Preliminary observations on harpacticoid copepods (Kauri and Odselius, unpublished) only show one receptor, comprising a cavity below the integument in the rostrum.

The deep receptors of the Copepoda (the second unit, the end organ A and the organ in the harpacticoids) thus show an essentially identical location. These receptors also have an identical structure as regards the individual elements, and the following characteristics are shared in common by the species of the Maxillopoda discussed here. Supporting cells, which enclose an extracellular cavity into which ciliated dendrites project, and cilia with terminations with a diameter of ca 100 nm and usually one central microtubulus. Individual deviations from this pattern are found on the organ level regarding the shape and the size of the organ. Differences are also found in the ciliary structure. The latter regards especially the Notodelphyidae (Dudley, 1972), including the absence of ramifications and the occurrence of septate desmosomes between the ciliary ramifications and the supporting cell membrane.

Thus with the exception of the multiciliated dendrites the structural characteristics of the deep receptor in the Copepoda are in agreement with those of the presumed oB in the Mystacocarida and Cirripedia.

The superficial receptors of the oB complex are found in the Copepoda and the Cirripedia. These receptors share an anterior location in the head. Structurally they are characterized by the ciliated dendritic terminals, glial and/or supporting cells, a more or less spacious extracellular cavity and a more or less pronounced participation of epidermal cells.

The supporting or glial cells terminate on the level of the dendritic terminations except in the Copepoda Notodelphyidae, where they cover the entire dendrite (Dudley, 1972). The cell is here penetrated by the cilia in a manner similar to that described for cilia penetrating an epidermal cell in Calanus (Elofsson, 1971). Apparently these two cell types perform similar functions in individual species. Distally the cilia are surrounded by epidermal cells or their processes. Direct apposition between ciliary and epidermal cell membranes occurs and in the notodelphyids also septate desmosomes are formed here. The individual variations in the extent of epidermal cell participation in the organ, either in the form of processes into the cavity or along the cuticle might be subject to changes during the moulting cycle, as shown for the organ i Balanus in the present paper. Thus the lack of epidermal elements close to the cuticle in Doropygus (Dudley, 1972) and the presence of processes of these cells in Calanus (Elofsson, 1971) might be explained as transitory phenomena during individual phases of the moulting cycle, which of course might influence the functional status of the organ. It appears that the precise extent of participation by epidermal cells in the organ must await a further examination of the changes during the moulting cycle. Until then a rather wide variation in the epidermal contribution to the organ must be accepted.

Assuming a more or less similar contribution to the organ by the supporting, the glial, and the epidermal cells in the individual species, the characteristic elements for each organ are to be found among the ciliated dendrites and the cuticular covering of the organ cavity. The two types of cilia found in the organ in Balanus might be compared to those of the two types of organ in the Copepoda. The ramifying cilia basally are reminiscent of the calanoid type and the slender cilia are similar to those of the notodelphyid organ. The latter comparison also involves the observed adhesion between individual cilia and between these and the epidermal cell membranes in Balanus, which is reminiscent of the desmosomal structures described from Doropygus. Special ciliary characteristics thus are found to tie the three organs together via the organ in Balanus.

The characteristics found in the cuticular covering of the organ are inconsistent. Relatively thin cuticle is found in the organ area in Balanus and Doropygus. Also in Calanus where the cuticle exceeds $1\ \mu\text{m}$ (Fig. 11, Elofsson, 1971), the thickness is reduced by pores from the internal surface. The remaining calanoids apparently have no such pores. The projection of the integument into frontal filaments in the receptor area in Balanus might have functional implications in increasing the surface and furthering possible mechanoreception, but it does not change the fundamental interrelation between the organ elements. Notwithstanding the differences in the cuticular covering, and the multiciliated dendrites of the Copepoda, the superficial receptors of the Maxillopoda are sufficiently well tied together.

From the characteristics, given above, for the deep and superficial receptors in the individual taxa of the Maxillopoda, regarding their localization and structure, it is possible to homologize each of the two receptors throughout the Maxillopoda. Both receptors satisfy two of the main criteria for homology (Remane, 1961).

The criterium of localization refers to the position in the head and to the connection with the protocerebrum.

The criterium of special qualities is also satisfied, but its significance is somewhat weakened for the superficial receptor, as similar receptors are found in quite different locations and connections, eg the aesthetasc hairs of the antennules (Ghiradella et al., 1968).

The significance of the criteria for both receptors gain in strength, as similar organs are known from a number of Crustacea outside the Maxillopoda.

Thus the close similarity in location and fine structural characteristics of the deep receptor can be widened to accommodate the oB among the Peracarida, as the characteristics can be compared feature by feature with those described from different peracarideans (Chaigneau, 1971, 1972; Kauri and Dahl, 1975; Dahl and Kauri, MS; Kauri, MS 2). Differences, apart from individual variation of a minor grade, are due mainly to differences in size and to the presence in the peracaridean organs of the neurone perikarya.

Also the criteria for the superficial receptor are accepted by a wider range of crustacean organs, viz the cavity receptor in Artemia (Elofsson and Lake, 1971; the sensory pore in Atyaephyra (Chaigneau, 1973) the sensory pore in Boreomysis (Kauri and Myhrberg, unpublished) and probably the sensory pore in Nebalia (Chaigneau, 1973 b).

Thus two systems of homologous receptors emerge, and are tentatively characterized as follows. The one, superficial receptor, comprises the cavity organ and the sensory pores. The other, deep receptor, comprises the oB.

As both the superficial and deep receptors, where present, are interconnected in a similar manner in the individual taxa, also the entire oB complex must be considered a homologous system of receptors. These homologies are partly found on conditions in the oB complex in crustaceans outside the Maxillopoda. A close discussion of these conditions among the Crustacea generally will be given elsewhere (Kauri, MS).

Of special interest here is the identification of the X organ in a wide range of species among the Copepoda (Elofsson, 1966). It was homologized with the X organ as conceived by Hanström (1947), which is identical with the concept of the oB (Amar, 1950; Gabe, 1966). In an analysis of the fine structure of this organ (Elofsson, 1971), it became evident that it really comprised a complex of one deep and two superficial receptors. A concept considerably wider than that of the oB. The deep receptor then was compared to the oB and one of the superficial receptors (second unit, Elofsson, 1971) was compared to the cavity receptor in Artemia (Elofsson, 1971; Elofsson and Lake, 1971; Dudley, 1972).

The homologization of the frontal filament base of the cirriped larvae with the oB (= SPX) in the Peracarida was made from light microscopical material (Kauri, 1966), and the organ in the Mystacocarida was also suggested as an homologue of the oB (= X organ) by Dahl and Elofsson (cf. Elofsson, 1966).

Although the cephalic receptors, considered here, combine into the homologous oB complex, strong individual characteristics remain with the Copepoda and Cirripedia.

Thus the multiciliated neurones of the organ complex in the former constitute a unique feature. In the Cirripedia the presence of different types of cilia in the superficial receptor and the communication between the cavities of the superficial and deep receptors also are unique individual characteristics. In the Mystacocarida finally, with the superficial receptor probably absent, the oB shows a good agreement with that of the Peracarida. The nerves emerging close to the median plane from the protocerebrum, should be regarded against the complete absence of eyes in the species examined.

These individual variations of the oB complex between the individual taxa among the Maxillopoda still must be considered with caution, as the information on the fine structure of the complex is concentrated to only a few species. Examination of a larger material is necessary to bring out the amplitude of structural variation.

It is intriguing to speculate over the significance of the characteristics of the organ complex in the Cirripedia. Are these larval adaptations, or do they represent a configuration with a significance phylogenetically? It might be argued that the oB is evolved from a superficial area with a sensory potential. For the present data on the embryology of the oB in Cirripedia are not known, but in Palaemonetes (Hubschman, 1963) has shown a vesicular component of the SPX (= oB) to develop in contact with the epidermis with a subsequent localization to a deeper level in the eye stalk.

The oB has been discussed repeatedly on earlier occasions in wider contexts by a number of authors (eg. Hanström, 1947; Dahl, 1963, 1965; Gabe, 1966).

The present paper brings the Maxillopoda more generally into the discussion and widens the concept of the superficial receptors of the oB complex to include the sensory pore/papilla.

It is not intended here to give a discussion of the different functions, considered possible in the cephalic receptors. One is given by Walker (1974) for the cirriped larvae, and Elofsson (1971) has introduced the idea of internal chemoreception for the oB, also considered in Anilocra (cf Chaigneau, 1974). A discussion on functional aspects will appear elsewhere (Kauri, MS).

It must be pointed out however, that the oB among the Maxillopoda always has been found in a position sufficiently close to the integument, to be able to function as a photoreceptor of a non-visual kind, as mentioned also by Walker (1974).

An interesting complication is introduced into the oB complex in the cirriped larvae. This is brought about, partly through the communication between the cavities of the superficial and the deep receptors, and partly by the situation that might arise in larvae between moults, where communications might open between the superficial receptor cavity and adjacent haemocoelic spaces. As mentioned earlier, this latter situation needs confirmation. Such conditions might have direct significance not only for chemoreceptory functions, which after all remain a strong possibility, but also for other receptory functions, while affecting the external chemical milieu of the, possibly receptory, ciliary membranes.

Another feature of interest, especially for mechanoreceptory functions, is the junctional apparatus observed between ciliary ramifications in the Doropygus organs (Dudley, 1972). These structures appear to be rather uncommon in the oB complexes described so far, but indications are for similar structures in the Balanus filament (Walker, 1974).

References

- Amar, R. 1950. Les formations endocrines cérébrales des Isopodes marins. C.R. Acad. Sci. Paris. 230:407-409.
- Baccari, S., Renaud-Mornant, J. 1974. Étude du système nerveux de Derocheilocaris remanei Delamare et Chappuis 1951 (Crustacée, Mystacocarida). Cahiers de Biol. Mar. 15:589-600.
- Bocquet-Védrine, J. 1972. Suppression de l'ordre des Apodes (Crustacés Cirripèdes) et rattachement de son unique représentant, Proteolepas bivineta, à la famille des Crinoniscidae (Crustacés Isopodes, Cryptonisciens). C.R. Acad. Sci. Paris. 275: 2145-2148.
- Boyde, A., Wood, C. 1969. Preparation of animal tissues for surface-scanning electron microscopy. Journ. Microsc. 90:221-249.
- Bresciani, J. 1965. Nauplius "Y" Hansen. Its distribution and relationship with a new cypris larva. Vidensk. Meddr. dansk naturh. Foren. 128:245-258.

- Cals, P., Delamare
Deboutteville, C., Renaud-
Mornant, J. 1971. Caractères anatomiques des Mystacocarides (Crustacés). Etude de Derocheilocaris remanei Delamare Deboutteville et Chappuis 1954. C.R. Acad. Sci. Paris. 272:3154-3157.
- Chaigneau, J. 1971. L'organe de Bellonci du Crustacé Isopode Sphaeroma serratum (Fabricius). Ultrastructure et signification. Z. Zellforsch. 112:166-187.
- . 1972. Particularités ultrastructurales de l'organe de Bellonci d'Anilocra frontalis Milne Edwards, Crustacé Isopode Flabellifère Cymothoïde. C.R. Acad. Sci. Paris. 274:1194-1197.
- . 1973. Fine Structure of the Sensory Pore Present in the Eyestalk of Crustacea Natantia. Z. Zellforsch. 145:213-227.
- . 1973 b. Données ultrastructurales sur le complexe pore sensoriel-organe de Bellonci de Nebalia bipes Fabricius Crustacé Leptostrace. C.R. Acad. Sci. Paris. 276:1753-1756.
- . 1974. Evolution ultrastructurale en relation avec l'état sexual, de l'organe de Bellonci autochtone et implanté, chez le Crustacé, Isopode hermaphrodite, Anilocra frontalis. C.R. Acad. Sci. Paris. 279:771-774.
- Dahl, E. 1952. Reports of the Lund University Chile expedition 1948-49, 7. Mystacocarida. Acta Univ. Lund, N.S. 48 (6):1-40.
- . 1963. Main evolutionary lines among recent Crustacea. In: Phylogeny and evolution of Crustacea. Museum of Comparative Zoology, Special Publ. Ed. H.B. Whittington and W.D.I. Rolfe. 1-26.
- . 1965. Frontal organs and protocerebral neurosecretory systems in Crustacea and Insecta. Gen. Comp. Endocrinol. 5:614-617.
- ., Kauri, T. MS. Observations on the fine Structure of the Organ of Bellonci (SPX) in Halice abyssi BOECK (Crustacea, Peracarida, Amphipoda).
- Dudley, P. 1972. The Fine Structure of a Cephalic Sensory Receptor in the Copepod Doropygus seclusus Illg (Crustacea: Copepoda: Notodelphidae). J. Morph. 138:407-432.
- Delamare Deboutteville, C., Chappuis, P.A. 1954. Recherches sur les Crustacés souterrains. II. Morphologie des Mystacocarides. Arch. Zool. exp. gén. 91:7-24.
- Elofsson, R. 1963. The nauplius eye and frontal organs in Decapoda (Crustacea). Sarsia. 12:1-68.

- Elofsson, R. 1965. The nauplius eye and frontal organs in Malacostraca (Crustacea). *Sarsia*. 19:1-54.
- . 1966. The nauplius eye and frontal organs in the non Malacostraca (Crustacea). *Sarsia*. 25:1-128.
- . 1971. The Ultrastructure of a Chemoreceptor Organ in the Head of Copepod Crustaceans. *Acta Zool.* 52:299-315.
- . 1971 b. Some observations on the internal morphology of Hansen's nauplius Y (Crustacea). *Sarsia* 46:23-40.
- , Lake, P. 1971. On the Cavity Receptor Organ (X-Organ or Organ of Bellonci) of *Artemia salina* (Crustacea; Anostraca). *Z. Zellforsch.* 121:319-326.
- Gabe, M. 1966. Neurosecretion. Pergamon Press. Oxford.
- Ghiradella, H., Cronshaw, J., Case, J. 1968. Fine Structure of the Aesthetasc Hairs of *Pagurus hirsutiusculus* Dana. *Protoplasma*. 66:1-20.
- Ha, H. 1970. Axonal Bifurcation in the Dorsal Root Ganglion of the Cat: A Light and Electron Microscopic Study. *J. Comp. Neur.* 140:227-240.
- Hanström, B. 1947. The brain, the sense organs and the incretory organs of the head in the Crustacea Malacostraca. *Acta Univ. Lund., N.F.* 58 (9): 1-45.
- Hauw, J.J., Berger, B., Escourolle, R. 1975. Ultrastructural Observations on Human Cerebral Capillaries in Organ Culture. *Cell Tiss. Res.* 163: 133-150.
- Hubschman, J.H. 1963. Development and function of neurosecretory sites in the eyestalks of larval *Palaemonetes* (Decapoda: Natantia) *Biol. Bull.* 125: 96-113.
- Kauri, T. 1962. On the frontal filaments and nauplius eye in *Balanus*. *Crustaceana*. 4: 131-142.
- . 1966. On the sensory papilla X organ in cirriped larvae. *Crustaceana*, 11: 115-122.
- . MS. The organ of Bellonci.
- . MS 2. The fine structure of the organ of Bellonci in *Diastylis rathkei* Kr. (Crustacea, Peracarida, Cumacea).
- , Dahl, E. 1975. Fine Structure of the Organ of Bellonci (SPX) in *Boreomysis arctica* (Krøyer) (Crustacea, Mysidacea). *Zool. Scr.* 4: 41-47.
- , Lake, P.S. 1972. The Structure of the Organ of Bellonci of the Syncarid Crustacean, *Anaspides tasmaniae* (Thomson). *Z. Zellforsch.* 132: 431-450.

- Millonig, G.J. 1961. Advantages of a phosphate buffer for OsO_4 solutions in fixation. J. appl. Phys. 32:1637.
- Nadelhaft, I. 1974. Microtubule densities and total numbers in selected axons of the crayfish abdominal nerve cord. J. Neurocyt. 3:73-86.
- Nilsson-Cantell, C.-A. 1921. Cirripeden-Studien. Almqvist & Wiksell. Uppsala.
- Pennak, R.W., Zinn, D.J. 1943. Mystacocarida, a new order of Crustacea from intertidal beaches in Massachusetts and Connecticut. Smiths. Misc. Coll. 103 (9). 1-11.
- Pitelka, D.R. 1974. Basal bodies and root structures. In: Sleight, M.A. (Ed). Cilia and Flagella. Academic Press. London. 437-469.
- Remane, A. 1961. Gedanken zum Problem: Homologie und Analogie, Praeadaptation und Parallelität. Zool. Anz. 165:447-465.
- Wagin, V.L. 1946. Ascothorax ophioctenis and the position of Ascothoracida Wagin in the system of the Entomostraca. Acta Zool. 27:155-267.
- Walker, G. 1974. The Fine Structure of the Frontal Filament Complex of Barnacle Larvae (Crustacea: Cirripedia). Cell Tiss. Res. 152:449-465.
- Walley, L.J. 1969. Studies on the larval structure and metamorphosis of Balanus balanoides (L.). Phil. Trans. B 256: 237-280.
- Young, R.W., Bok, D. 1969. Participation of the retinal pigment epithelium in the rod outer segment renewal process. J. Cell. Biol. 42:392-403.

The fine structure of the organ of Bellonci in Diastylis rathkei Kr.
(Crustacea, Peracarida, Cumacea).

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Abstract

The oB in Diastylis rathkei has been examined using light and electron microscopy, and found to have characteristics typical for the peracaridean organ with a large amount of tubular ciliary ramifications. Lack of dendritic ramifications and a distribution of the neurone perikarya over most of the organ wall give a closer association to the type of organ found among the Isopoda rather than to that of the Mysidacea-Amphipoda. Indications of neurone turnover and an interpretation other than neurosecretory of the prominent secretory mechanism in the organ are discussed.

Introduction

The histology of the oB in *Diastylis rathkei* has been described by Oelze (1931) and Ståhl (1938). The organ is located centrally in the anterior part of the head, ventral to the fused compound eyes. It consists of two vesicular units, derived from paired anlagen, as indicated by the paired innervation (Hanström, 1947). The paired oB in *D. rathkei* thus are fused, like the compound eyes. In the adult the organs are located with one posterior to the other. The posterior organ lies somewhat dorsal to the anterior one. The organs were considered to be statocysts (Oelze, 1931) until identified as oB (= X organ, Ståhl, 1938). The two nerves from the oB are thought to connect to the medulla terminalis, though the exact point of connection is difficult to identify due to fusions in the optic centra (Gabe, 1966). The present examination of the fine structure of the oB in *D. rathkei* was undertaken as part of a comparative examination of the oB among the Crustacea.

Material and method

Specimens of *D. rathkei* were dredged from the Sound in a locality immediately to the north of the island of Ven on a mixed soft bottom at ca 20 m depth. The collecting was carried out from the research vessel "Carolina", belonging to the University of Lund.

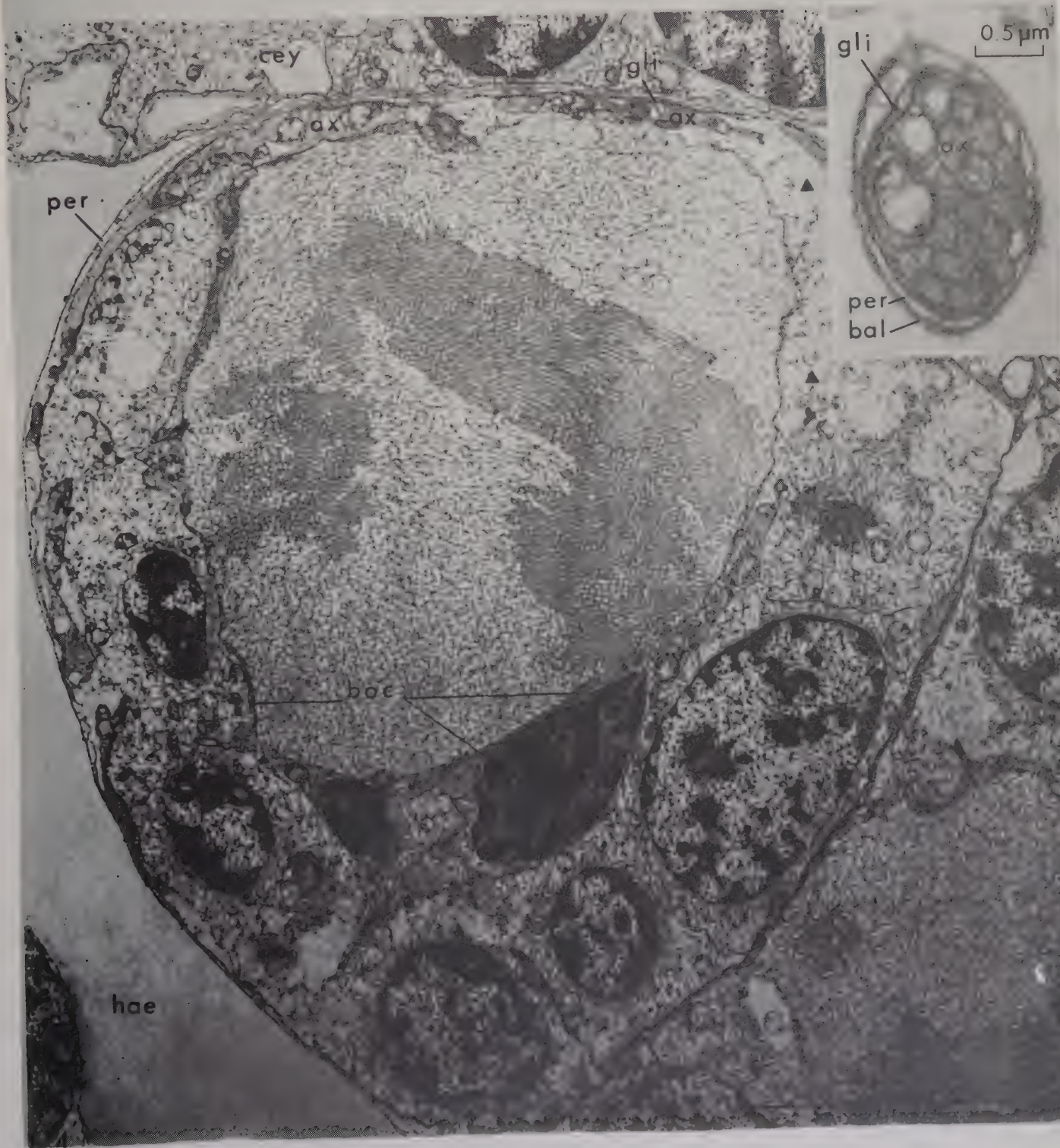
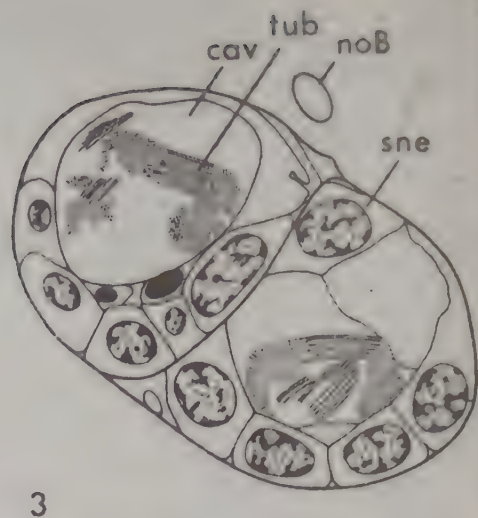
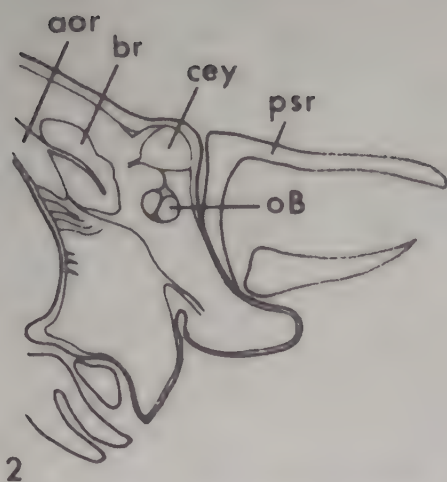
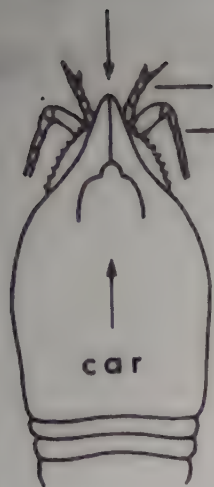
The material obtained consisted of females, a number of which were ovigerous. The latter were kept in the laboratory in small aquaria with cooled circulating sea water, and juvenile specimens were hatched. Newly hatched juveniles were collected each morning, why the age of the juveniles examined cannot exceed a maximum of 24 hours.

Material for light microscopy was fixed in Bouin's ethanolic fluid (Romeis, 1968:307), embedded in paraffin wax and cut on a rotary microtome. Heidenhain's Azan (Romeis, 1968:1530) and chrome haematoxyline-phloxine (Gomori, 1941) were used in staining.

Fig. 1 Dorsal view of head and thorax. arrows - plane of section, shown in Fig. 2. a - antennula; a - antenna; car - carapax; (After Oelze, 1931).

Fig. 2 Median section of head (cf Fig. 1). aor - aorta; br - brain; cey - compound eyes; oB - organ of Bellonci with nerve; psr - pseudorostrum; (After Oelze, 1931).

Fig. 3 and 4 *D. rathkei* juv. Median section through oB. Plane of section and position of organ as in Fig. 2. The diagram, Fig. 3, is from an electron micrograph, part of which is shown, Fig. 4. Inset: The nerve from one of the oB in cross section. ax - axon; bal - basal lamina; boc - bordering cells; cav - organ cavity; cey - compound eye; gli - glial cell; hae - haemocoel; noB - nerve from one of the oB; per - perilemmal cell; sne - sensory neurone; tub - tubular ciliary branches; triangles - possible area of neurone degradation.



Intact oB for electron microscopy were dissected from the adults under 2.5 % glutaric aldehyde, and buffered to pH 7.3 in phosphate buffer (Millonig, 1961), while juveniles were decapitated in the same solution. The preparations were fixed in the same fixative for 1 - 2 hours, and postfixation was carried out in 1 % OsO₄, made up in the same buffer, during another 1 - 2 hours. Contrast was added by immersion in 0.5 % uranylacetate and 1 % phosphotungstic acid in absolute ethanol during dehydration. Vestopl W was used for embedding and sections were cut on an LKB Ultratome 8801 A. The sectioned material was examined in Philips EM 300. The use of honeycomb grids facilitated examination of shorter series of sections.

Results

Light microscopical observations

The location of the oB and their general structure are found to agree with the description given by Oelze (1931). While the adult, fused organ is nearly spherical, that of the juveniles is elongated along the axis through the two component organs. In the adults the wall separating the two organ cavities, is thin without perikarya in contrast to that of the juveniles, where perikarya might be found in this location (cf Fig. 4). The perikarya of neurones and supporting cells are located to the organ wall. The number of neurone perikarya apparently is unchanged, approximating 20 in both juveniles and adult females, while the perilemmal and supporting cell material increases with age. In the cavity fibrillar material is present. Also, the cavity contents stain heavily with the haematoxyline component of the Gomori technique. The reaction apparently is not located to the fibrillar material, which appears lighter in the sections. Externally the organ is surrounded by haemocoel or strands of connective tissue, which attach to the organ wall. The nerves leave the organs close to the median line dorsally, where the two organs meet.

Electron microscopical observations

The examination of the oB fine structure was facilitated in using the juvenile material, where the organ size was smaller. The structure of the organ, as seen in the light microscope (cf Fig. 2), is directly recognizable in the electron microscope, as represented by the diagram in Fig. 3, which is based on the section shown in Fig. 4.

The oB comprises elements from at least four, probably five sources: the perilemmal cells, the basal lamina, the bordering cells, the glial cells and the sensory neurones.

The perilemmal cells in young specimens apparently form a thin layer of cell processes, covering the organ and the nerve (Fig. 4, 5). This layer is in continuity with the perilemmal cells of the protocerebrum. These cells have a more or less electronlucent cytoplasm. In older specimens, this layer is a few cell processes thick, with desmosomal contacts between the apposed membranes (Fig. 6). Also, in the older specimens, the innermost processes of these cells contain bundles of microtubules, arranged parallel to the organ surface.

The basal lamina makes up the external surface of the organ. It is very thin in young specimens (Fig. 4, 5) but approximates 100 nm in older ones (Fig. 6). The lamina might be formed by the perilemmal cells or it might be contributed by haemocytes, as suggested for certain Insecta (cf Neville, 1974).

The bordering cells have small perikarya with dense nuclei of an elongated or angular shape (Fig. 4, 7). The cytoplasm is dense in comparison with that of the sensory neurone or the perilemmal cell. Individual bordering cells might show a different density of the cytoplasm. Thin processes from these cells are found to cover the inside of the cavity wall (Fig. 5, 7, 8), except where the dendritic terminals penetrate (Fig. 10, 11). Processes are also found between the sensory neurones. The cytoplasm has rough endoplasmic reticulum and frequently is vacuolated (Fig. 11). In adults the wall between the two organs is made up from bordering cell processes with occasional processes from glial cells intervening.

The glial cell occupies an intermediate position to the two types of cells described (Fig. 5), wrapping the sensory neurones on the external side, but internal to the perilemmal cells. Processes from glial cells also intervene between the perilemmal cell process and the axons in the nerve (Fig. 4).

The sensory neurone perikarya are located in the organ wall. The cytoplasm of the neurone is relatively electron lucent, with mitochondria, sparse reticulum of smooth and rough types, golgi bodies and occasionally granular material ca 15 nm (Fig 8). Axons and dendrites are seen to emerge from the perikarya. The bordering and glial cell processes usually cover the perikarya, but smaller areas of membrane of adjacent perikarya might be directly apposed to each other. In the organs occasionally areas are encountered, which might indicate a degradation of entire sensory neurones. These areas then are contained between bordering cell and sensory neurone membranes and contain scattered electron dense material (Fig. 4, upper right).

Fig. 5 *D. rathkei* juv. Cavity wall close to cuticle anteriorly. bal - basal lamina; boc - bordering cell; cut - cuticles of head and pseudorostrum; gli - glia cell; hae - haemocoel; per - perilemmal cell; psr - pseudorostrum; sne - sensory neurone.

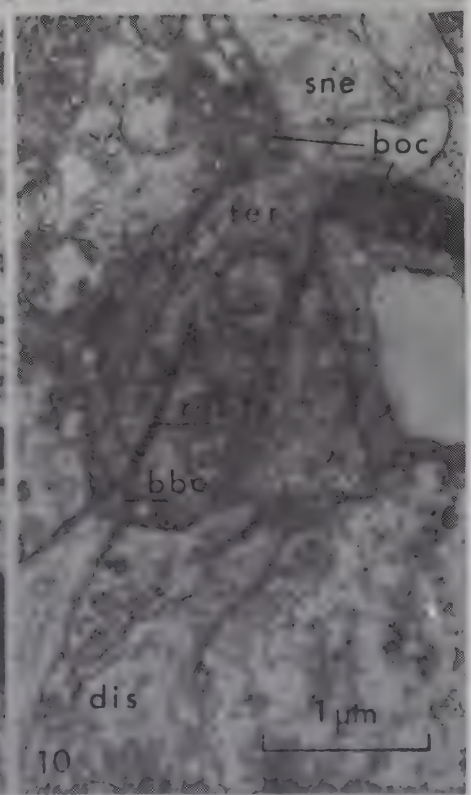
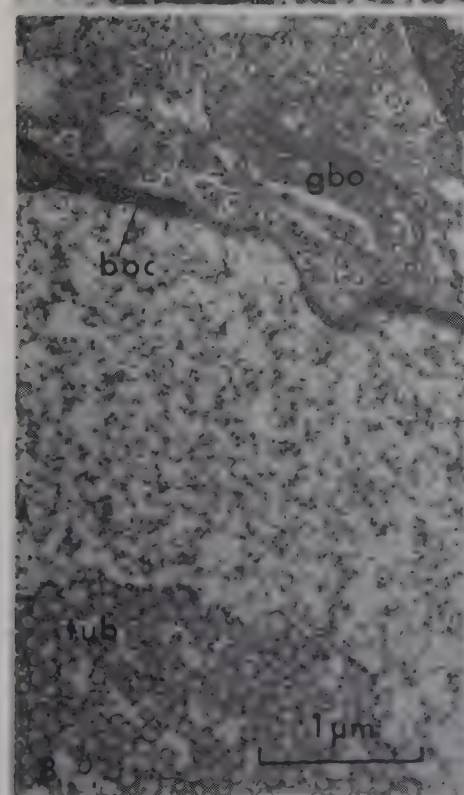
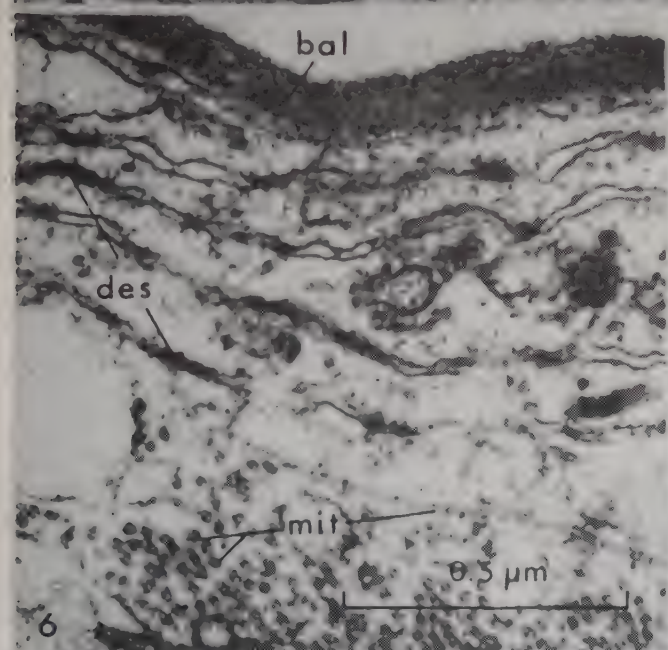
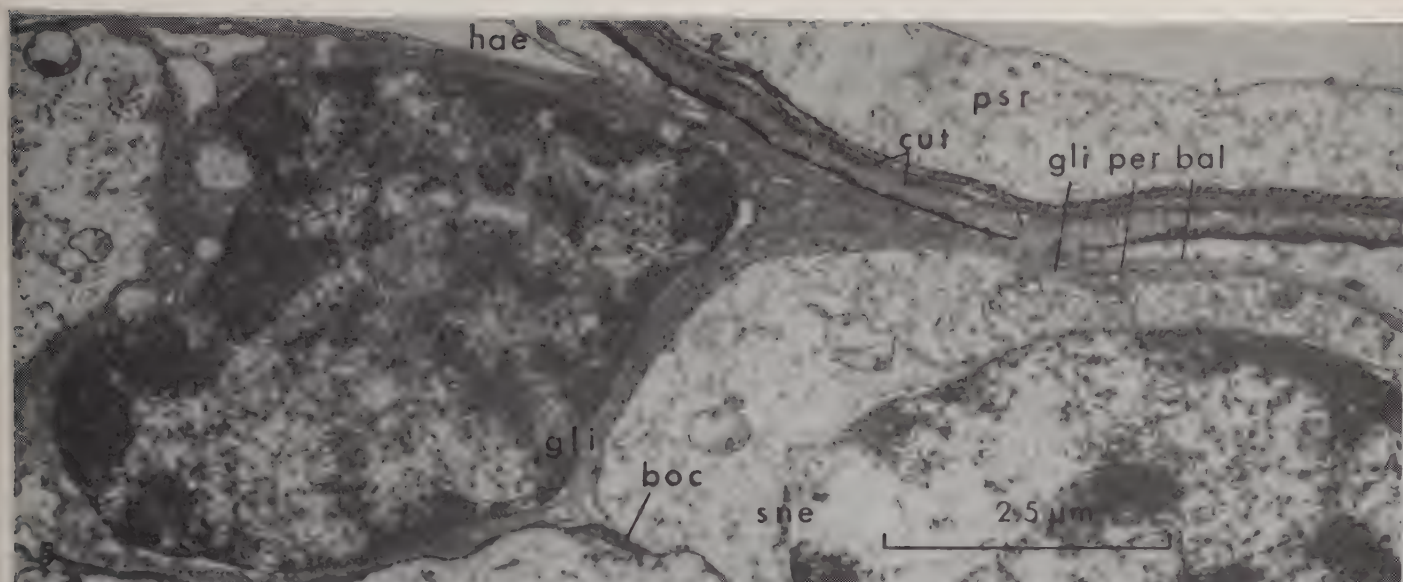
Fig. 6 *D. rathkei* ad. ♀. Part of cavity wall showing several layers from perilemmal cells. The basal lamina (bal) borders to the haemocoel. des - desmosomal structures; mit - microtubules.

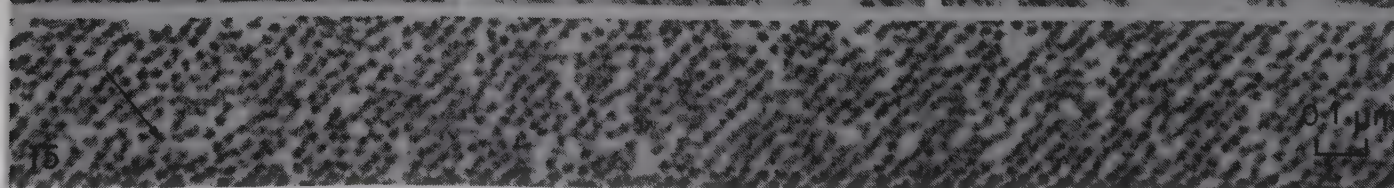
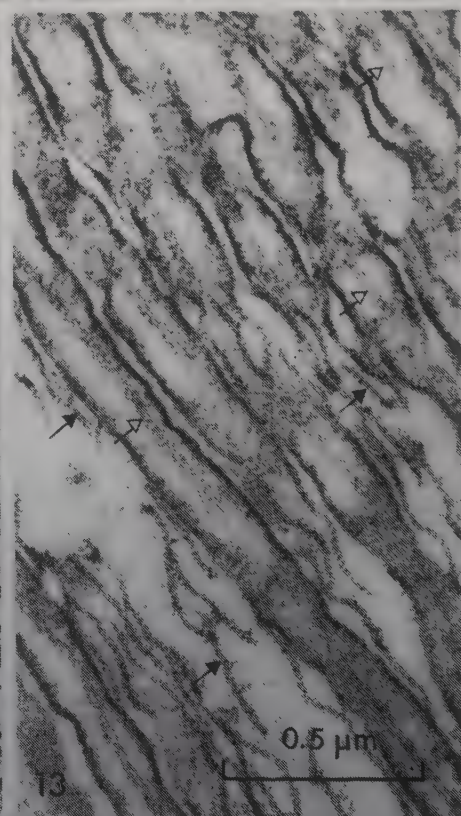
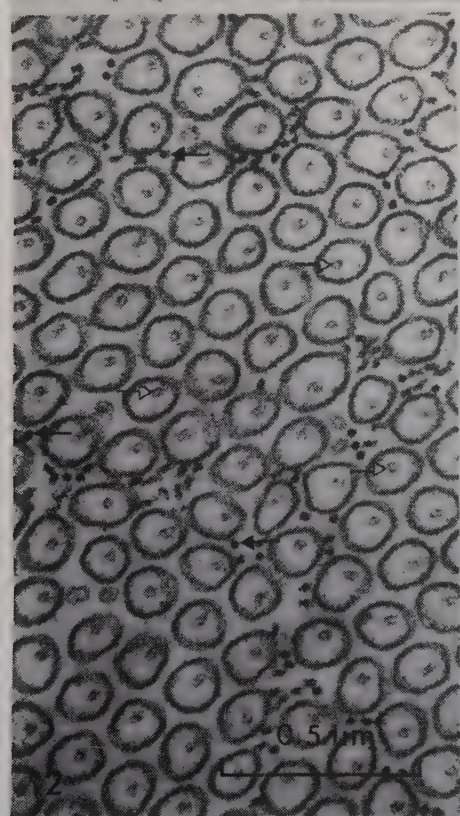
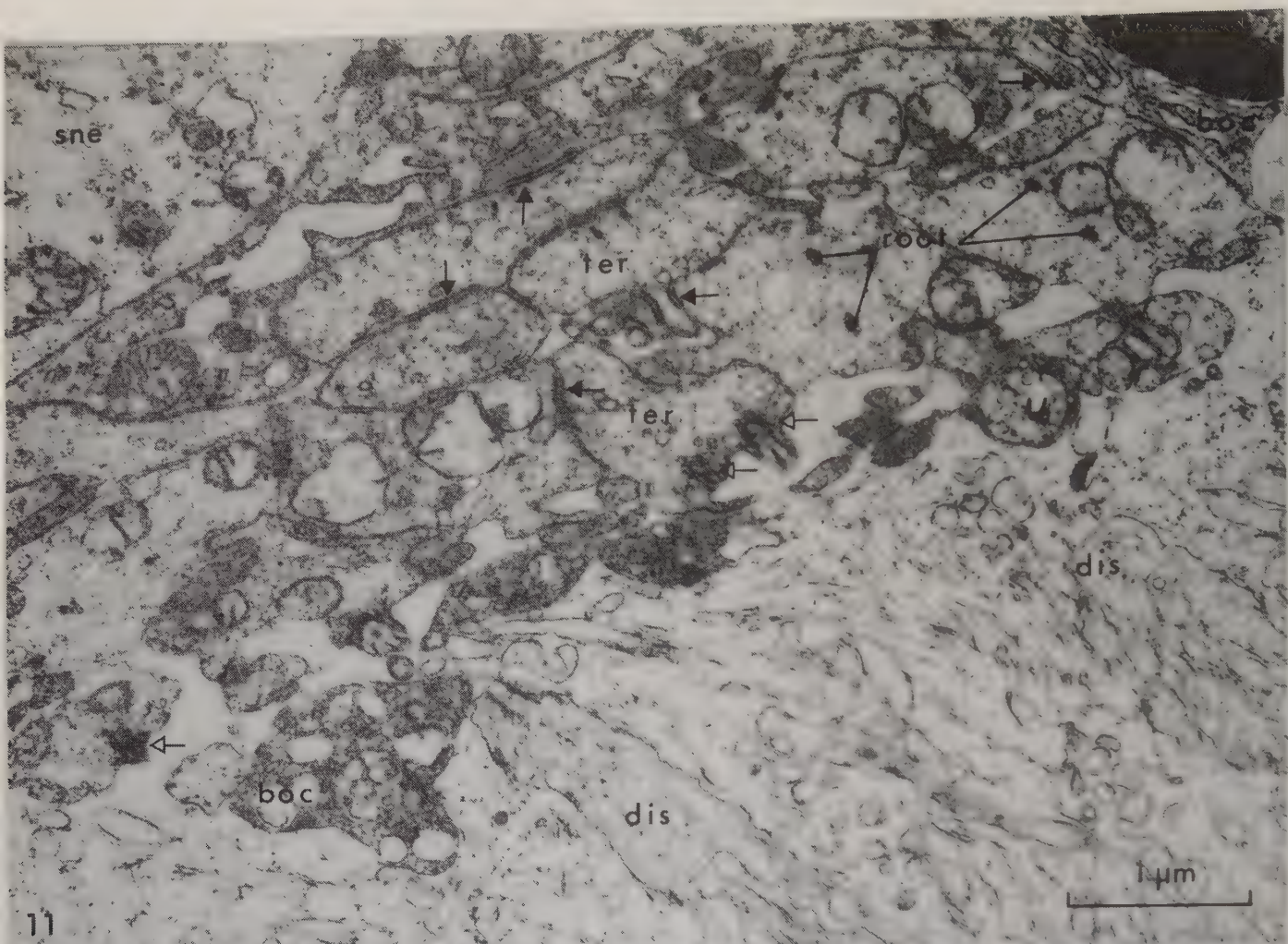
Fig. 7 *D. rathkei* juv. Bordering cell perikaryon. Two superposed processes from bordering cells (1, 2).

Fig. 8 *D. rathkei* juv. Neurone perikaryon with golgi body (gbo), granular material in the cytoplasm and nucleus with perinuclear cistern on upper right. boc - bordering cell process; tub - tubular ciliary branches.

Fig. 9 *D. rathkei* juv. Dendrite (den) connecting to perikaryon of sensory neurone. boc - bordering cell processes.

Fig. 10 *D. rathkei* juv. Cilium originating from dendritic termination (ter) in direct contact with perikaryon of sensory neurone (sne). The nucleus is seen on the upper right. bbo - basal body; boc - bordering cell; dis - distended ciliary shaft; root - rootlet.





The axons are found close to the organ periphery, sheathed by glial processes. Axons have been followed into the nerve, where their number approximates that of the neurone perikarya found in the organ (Fig. 4, inset). The axon diameter dwindles until in the nerve it approximates 200 nm with occasional distensions. No glial processes are found between individual axons.

The dendrites are seen to leave the perikarya closer to the organ cavity, and to follow the cavity lining internal to the perikarya. The dendrites are sheathed by bordering cell processes (Fig. 9) until their terminations. Usually a number of dendrites is seen to terminate close to one another. Such a terminating area has a more or less lateral location in the cavity and there apparently are two such areas. The number of dendrites contributing to one of these (Fig. 11) approaches 10. In the terminating area, processes from bordering cells are found among the dendrites. Junctional structures are found between the individual dendrites and between these and the bordering cell processes. The terminals have rather a modest size (ca $1\text{ }\mu\text{m}$ by $2\text{ }\mu\text{m}$), few mitochondria, occasional vesicular material and scarce granules of the type found in the perikarya. Where a neurone perikaryon lies close to a terminating area, the dendritic terminal is formed directly from the perikaryon (Fig. 10). A pair of cilia originates from each dendrite.

The cilia (Fig. 10, 11) have basal bodies (diameter ca 160 nm) with rootlets of a transverse periodicity of ca 60 nm. One rootlet apparently attaches to each basal body. The pairs of rootlets are seen in transversely sectioned dendrites as dark, rounded profiles (fig. 11). A short neck region with an axoneme of the 9 + 0 type is observed. Distally in the more or less conically distended cilia ($1\text{ }\mu\text{m}$ by $2\text{ }\mu\text{m}$, ca) vesicular material ($100 \pm 75\text{ nm}$) is found among predominantly longitudinally oriented microtubules. Also small amounts of granular electron dense material are observed in the shafts. The ramification of the cilium is successive, and the thicker branches ramify into long tubular branches, ca 100 nm in diameter terminally and with one microtubulus more or less centrally (Fig. 12, 13). The length of these branches has been observed to approach 20 μm .

The distal regions of the ciliary branches in certain specimens are locally distended (Fig. 14). These distensions give an annulated appearance to the tubular branches, and might exceed the diameter of the branch by a factor of ca 3. Apart from microtubules the distensions also contain vesicular material occasionally.

Fig. 11 *D. rathkei* juv. Area of ciliary origin. At least nine dendritic terminations (ter) are identified with basal bodies (open arrows) and junctional structures (filled arrows). Bordering cell processes (boc) intermingle with the dendrites. dis - distended ciliary shaft; root - rootlets; sne - sensory neurone.

Fig. 12 and 13 Tubular ciliary branches in cross (Fig. 12) and longitudinal section (Fig. 13), with microtubules (open arrows) and associated filaments (filled arrows).

Fig. 14 Area of locally distended tubular branches (arrows); ves - vesicular material.

Fig. 15 Area of aggregated filaments in cross section. arrow - direction of cut.

A terminal degradation of the branches appears to be operating especially in areas that are rich in distended branches. The degradation involves pinching off of segments of the branches, which then attain a vesicular shape.

The cavity contents, apart from the ciliary branches, also include a conspicuous filament component ca 15 nm in diameter. The filaments occur either in small groups among the tubular branches (Fig. 12, 13) or they might aggregate into large bundles (Fig. 15). Occasionally the aggregation of filaments might give a paracrystalline impression in cross sections. The filaments appear to be built up from subunits which might be arranged to form a spiral structure. This is indicated, in higher magnifications, by higher electron densities locally. These, denser, areas appear to be located in a zig-zag fashion along the filament axis. The filaments are found close to the membranes of both the ciliary branches and the bordering cells.

Discussion

The examination of the oB in D. rathkei reveals an organ, typical for the Peracarida, with a cavity enclosed by bordering cell processes and neurones of a sensory type with their cilia ramifying into the characteristic tubular branches of ca 100 nm diameter.

The organ is located in a sinus of the haemocoel ventral to the compound eyes. (Oelze, 1931). The haemolymph in the sinus is supplied from the antennules, eyes, and probably from part of the brain after having left the arterial vessels. The drainage is posteriorly on the dorsal and lateral sides of the alimentary tract.

The fine structure of the cumacean organ most closely resembles those organs described from the Isopoda (Chaigneau, 1971, 1972) in having only a single cavity with the sensory neurones more or less evenly distributed in the cavity walls.

Also the relatively short dendrites, which sometimes are entirely lacking, leaving only the small dendritic swelling directly from the sensory neurone perikaryon, are a characteristic reminiscent of the situation in the Isopoda.

Noticeable ramifications from the dendrites, as found in Boreomysis arctica (Kauri and Dahl, 1975) and Halice abyssii (Dahl and Kauri, MS), are lacking, leaving a relatively small amount of dendritic membrane directly exposed to the cavity contents. This feature is also shared with the Isopoda, as is the apparent lack of mitochondrial concentrations to the areas of ciliary origin in the dendrites.

Two further characteristics are directly comparable to those described in Anilocra frontalis (Chaigneau, 1972) viz the successive type of ramification of the cilia and the filamentous inclusions of the cavity.

The concentration of the dendritic terminals to limited areas of the cavity wall are described for the first time. These areas are indicative of a level of organization of the oB in D. rathkei, unusual in the oB morphology. However, the functional significance of this feature is difficult to estimate, assuming a receptory function involving mechanisms in the ciliary membranes, as the characteristic random distribution of the ciliary membranes is reestablished by the curving of the individual bundles of ciliary branches in the cavity.

The indications of a degradation of sensory neurone perikarya in the organ wall, is reminiscent of the situation in Sphaeroma serratum (Chaigneau, 1971). Such a process might be interpreted as one of possible mechanisms operating in the renewal of sensory elements. In aquatic vertebrates a periodic replacement of receptor elements is known from the olfactory epithelium (cf Laverack, 1974) and a turnover of sensory elements, also involving the exchange of entire neurons, is signalled from olfactory receptors in the frog, pigeon, mouse, and rat (Graziadei and Metcalf, 1971; Graziadei, 1974). In D. rathkei turnover also appears to be operating on the organelle level, as indicated by the degrading of the tubular branches by terminal vesiculation. The fate of the vesiculated ciliary membranes cannot be assessed with certainty, but vacuoles of a probably lytic function in the bordering cell cytoplasm might indicate a phagocytic process in these cells. Similar observations have also been made by Chaigneau (1971), regarding the bordering cells.

The nature of the distensions or annulations along the ciliary branches has been discussed repeatedly (Ghiradella et al, 1968; Elofsson, 1971). Such distensions apparently are a common feature in this type of ciliary receptors, and they probably are not artefacts, as they persist in preparations after freeze-substitution as well as after chemical fixation in aesthetascs of Pachygrapsus crassipes (Frisch and Everingham, 1972).

The strong reaction to the Gomori haematoxylin resembles that reported from B. arctica (Dahl and v. Mecklenburg, 1969; Kauri and Dahl, 1975) and from H. abyssii (Dahl and Kauri, MS). Indications of secretory activity have also been reported from the Isopoda (Amar, 1951; Chaigneau, 1971). A further wealth of observations, indicating a strong secretory activity in the oB among the Crustacea is referred by Gabe (1966). This has earlier been attributed to contents of neurosecretory material, but the peracaridean oB appears not to be involved in any neurosecretion of the types known so far, as shown by the fine structural detail of the organ (cf Chaigneau, 1971). The only observations that might be interpreted as indicative of a neurosecretory activity, are those regarding the membranebound granular material in the axons (Dahl and Kauri, MS), and would in all probability not involve a release to the organ cavity. The observations made by Smith (1974), describing neurosecretory elements in the oB of Carcinus maenas are difficult to interpret, as the interrelations of the individual elements are not shown fully, and will be discussed in more detail elsewhere (Kauri, MS). A significance, other than neurosecretory of the secretory material in the oB cavity, might be conceived however. It is to be expected that the large amount of sensory membranes in the organ cavity raises demands for metabolites, necessary for the maintenance of the functional state of these membranes. Apart from a supply through the ciliary base, a complementary supply of metabolites might be conceived, involving secretion from the bordering cells. A similar mechanism might be expected to operate in the superficial receptors of the oB complex (Elofsson and Lake, 1971; Kauri, MS 2).

The small dimensions of the axons ($0.2\ \mu\text{m}$) and the absence of intervening glia in the nerve from the oB are characteristic of D. rathkei. Small dimensions ($0.6\ \mu\text{m}$) also have been encountered in the oB axons in H. abyssi (Dahl and Kauri, MS). Laverack (1974) gives small dimensions ($0.1 - 0.5\ \mu\text{m}$) and a lack of individual glial investment as characteristics of olfactory axons. These observations in the peracaridean oB should be considered when discussing the nature of its sensory function.

References

- Amar, R. 1951. Formations endocrines cérébrales des Isopodes marins et comportement chromatique d'Idotea. Ann.Fac.Sci. Marseille. 220:171-305.
- Chaigneau, J. 1971. L'organe de Bellonci du Crustacé Isopode Sphaeroma serratum (Fabricius). Ultrastructure et signification. Z. Zellforsch. 112:166-187.
- . 1972. Particularités ultrastructurales de l'organe de Bellonci d'Anilocra frontalis Milne Edwards, Crustacé Isopode Flabellifère Cymothoide. C.R. Acad. Sci. Paris. 274:1194-1197.
- Dahl, E., Kauri, T. MS. Observations on the fine Structure of the Organ of Bellonci (SPX) in Halice abyssi BOECK (Crustacea, Peracarida, Amphipoda).
- Dahl, E., von Mecklenburg, C. 1969. The Sensory Papilla X-organ in Boreomysis arctica (Krøyer) (Crustacea Malacostraca Mysidacea). Z. Zellforsch. 101:88-97.
- Elofsson, R. 1971. The Ultrastructure of a Chemoreceptor Organ in the Head of Copepod Crustaceans. Acta Zool. 52:299-315.
- ., Lake, P.S. 1971. On the Cavity Receptor Organ (X-Organ or Organ of Bellonci) of Artemia salina (Crustacea; Anostraca). Z. Zellforsch. 121:319-326.
- Frisch, D., Everingham, J.W. 1972. Fine structure of crab olfactory cilia: non-chemical fixation; environmental effects. In: Olfaction and Taste IV, Schneider, D. (ed). Wissenschaftliche Verlagsgesellschaft MBH. Stuttgart. 5-12.
- Gabe, M. 1966. Neurosecretion. Pergamon Press. Oxford.
- Ghiradella, H., Cronshaw, J., Case, J. 1968. Fine Structure of the Aesthetasc hairs of Pagurus hirsutiusculus Dana. Protoplasma. 66:1
- Graziadei, P.P.C. 1974. The olfactory and taste organs of vertebrates: a dynamic approach to the study of their morphology. In: Transduction Mechanisms in Chemoreception. Poynder, T.M. (ed). Information Retrieval Limited. London. 3-14.

- Graziadei, P.P.C., Metcalf, J.F. 1971. Autoradiographic and Ultrastructural Observations on the Frog's Olfactory Mucosa. *Z. Zellforsch.* 116:305-318.
- Hanström, B. 1947. The brain, the sense organs and the incretory organs of the head in the Crustacea Malacostraca. *Acta Univ. Lund., N.F.* 58 (9):1-45.
- Kauri, T. MS. The organ of Bellonci.
- . MS 2. The fine structure of the organ of Bellonci in the Crustacea Maxillopoda, especially Balanus improvisus Darwin (Maxillopoda Cirripedia) and Derocheilocaris remanei Delamare and Chappuis (Maxillopoda Mystacocarida).
- ., Dahl, E. 1975. Fine Structure of the Organ of Bellonci (SPX) in Boreomysis arctica (Krøyer) (Crustacea, Mysidacea). *Zool. Scr.* 4:41-47.
- Laverack, M.S. 1974. The structure and function of chemoreceptor cells. In: Chemoreception in Marine organisms. Grant, P.T., Mackie, A.M. (eds). Academic Press. London. 1-48.
- Millonig, G.J. 1961. Advantages of a phosphate buffer for OsO_4 solutions in fixation. *J. appl. Phys.* 32:1637.
- Neville, A.C. 1975. Biology of the Arthropod Cuticle. Springer-Verlag. Berlin.
- Oelze, A. 1931. Beiträge zur Anatomie von Diastylis rathkei Kr. *Zool. Jb., Abt. Anat.* 54:235-294.
- Romeis, B. 1968. Mikroskopische Technik. R. Oldenbourg. München.
- Smith, G. 1974. The Ultrastructure of the Organ of Bellonci of Carcinus maenas (Crustacea: Decapoda). *Cell Tiss. Res.* 155:127-134.
- Ståhl, F. 1938. Über das Vorkommen von inkretorischen Organen und Farbwechselhormonen im Kopf einiger Crustaceen. *Acta Univ. Lund. NF* (2) 34 (12):1-20.

Observations on the fine Structure of the Organ of Bellonci (SPX)
in Halice abyssii BOECK (Crustacea, Peracarida, Amphipoda)

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Abstract

Dahl, Erik and Kauri, Tiit (Zoological Institute, University of Lund, S-223 62 LUND, Sweden). Observations on the fine structure of the organ of Bellonci (oB, SPX) in Halice abyssii Boeck (Crustacea, Amphipoda). The organ of Bellonci in Halice abyssii Boeck is described. It belongs to the peracaridean type of organ with tubular ciliary ramifications. Each organ comprises five organ units, each with a thin wall and a central cavity. The innervation is derived from the medulla terminalis region of the protocerebrum and the sensory neurones are arranged in one group with the dendrites diverging towards the organ units. The sensory membranes are formed through branching of the modified cilia in the organ cavities. Apart from the sensory neurones perineural, bordering, and glial cells are found in the organ. On comparison with earlier described peracaridean organs the greatest similarities are found to be with those of the Mysidacea.

1. Introduction

The organ of Bellonci of the Amphipoda has been described with the light microscope by several authors (Gamroth, 1878; Claus, 1887; Mayer, 1882; Della Valle, 1893; Schmalz, 1914; Zawadsky, 1915; Langenbuch, 1928; Thore, 1932; Gräber, 1933). The organ was given different names and different interpretations were given as to the function, among which acoustic, glandular, and statocyst functions were suggested.

Originally the organ was described as a frontal organ (Gamroth, 1878) and this name has repeatedly been used for the organ among the Amphipoda. However, the concept of the crustacean frontal organs has been analyzed more recently (Elofsson, 1963, 1965, 1966 and in this analysis it was shown that frontal organs are lacking among the Amphipoda (Elofsson, 1965).

The homology of the organ in the Amphipoda with the oB (Amar, 1950) has been signalled relatively recently (Dahl, 1963; Elofsson, 1965). As there exist several synonyms of the oB, viz X organ (Hanström, 1947), pars distalis X organi (Carlisle & Passano, 1953), and SPX organ (Knowles & Carlisle, 1956), the reader is referred to a discussion of oB nomenclature by Gabe (1966).

Recently an organ has been described from Rivulogammarus which is placed in an intermediate position between an oB and a frontal organ (Baid et al., 1972, 1974).

A description of the ultrastructure of the organ of Bellonci in the Amphipoda was considered interesting partly against the background given for the organ among the Amphipoda and partly as part of an examination of the oB among the Crustacea.

2. Material and methods

The specimens of Halice abyssii and Eurythenes gryllus were collected from waters off Biologisk Stasjon, Espesrend, Norway. The collection was undertaken in Raunefjord at a depth of 200 - 250 metres using a Milch's net. Material of Gammarus locusta was collected from the seashore of the Sound in the Landskrona area and serially sectioned material of this species was examined from the collection in the Zoological Institute, Lund.

When processing for the light microscopy the specimens were immersed in Bouin's ethanolic fixative according to Dubosq - Brasil (Romeis, 1968: § 307) for six hours or longer. Embedding was carried out in paraffin wax and sections were cut on a rotary microtome. The stains used were Heidenhain's Azan, Bodians's silver impregnation (Romeis, 1968: §§ 1530, 1854), and the chrome haematoxyline-phloxine (Gomori, 1941).

The preparations for electron microscopy comprised careful decapitation of the specimens under glutaric aldehyde at 2.5 %, followed by fixation in the same fixative for 1.5 hrs and a postfixation for 1.5 hrs in 1 % osmic tetroxide. Phosphate buffer (Millonig, 1961) was used for preparing the fixatives and for washing. Contrast was routinely added by immersing the specimens in uranylacetate (0.5 %) and phosphotungstic acid (1 %) in absolute ethanol during dehydration. The specimens were imbedded in Westopal V and sectioned on an LKB Ultratome 8801 A. For examination of the sections either Hitachi HS-7S or Philips EM 300 were used.

Heads of G. locusta for scanning electron microscopy were fixed in 4 % neutral formol, dehydrated in an ethanol series and dried via toluol at 80° C (Dahl, 1972). The specimens were examined under the Cambridge Stereoscan Mk III.

The observations are generally made on specimens of H. abyssi. Observations on E. gryllus or G. locusta are noted individually.

3. Observations

The head of H. abyssi is shown in lateral outline (Fig. 1). In a sagittal section of the head the organ of Bellonci is found in an anterior position to the brain and dorsal to the point of attachment of the antennulae (Fig. 2). The organ is spindle-shaped with the anterior end located medio-dorsally and the posterior end latero-ventrally. The entire organ is situated between connective tissue strands with a largest diameter of 50 - 100 μm and a length of 150 - 200 μm (Figs. 2, 4).

3.1 Light microscopical observations

The organ, the nerve, and the brain are covered by a thin perineurium to which surrounding connective tissue attaches (Fig. 2). A few flattened nuclei of the perineural cells are found (fig. 6).

Both ends of the organ taper into tissue strands which appear to terminate close to the cuticle or in contact with it at least posteriorly. No lumen is found in these structures. The surface of the cuticle in the corresponding areas in G. locusta was examined under the scanning electron microscope. No pores were revealed which might represent openings to the exterior of ducts from the oB.

The neurone perikarya of the organ are concentrated into one group antero-medially numbering about 20 - 30 neurones. This group is situated ventro-medially to the anterior tapering termination of the organ. Posterior to the perikarya the axons and the dendrites are found and postero-laterally the remainder of the organ is formed by about five identically built organ units, each with a central cavity which contains fibrillar material. The long axes of the organ units diverge slightly posteriorly (Figs. 3, 4, 7).

The nerve emerges from the organ in a point posterior to the neurone perikarya. It comprises the axons of the neurones and has a roughly posterior direction except close to the perikarya, where it traverses in an obliquely medial direction. As a consequence horizontal and sagittal sections pass out of the nerve close to the perikarya (Figs. 3 - 6).

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The dendrites leave the perikarya almost parallel to the axons, but soon curve in a lateral direction towards the proximal ends of the organ units. Depending on which unit is concerned, the dendrites curve more or less in a dorsal or ventral direction (Fig. 5). The dendrite diameter is 3 μ m or less before reaching the units.

In specimens impregnated with silver according to Bodian the dendrites are seen as dark dots or streaks depending on their plane of sectioning (Fig. 6). Also stained in these specimens are the axons and the basal, distended parts of ciliary shafts in the cavities. The axons can be traced into the medulla terminalis, where they are found in a dorsal position (Fig. 6). Two fibres in this region appear to have a larger diameter than that of the average axon. Especially clear impregnations were obtained in E. gryllus, where axons could be traced into the proximity of the optic tract.

The cytoplasm of the neurone perikarya reacts weakly with the hematoxyline of the Gomori technique while the reaction is intense inside the cavity. Inside the cavities also acidophilic inclusions are observed in Azan (Fig. 3, 4).

Close to the organ hemocoelic spaces are found. The supply of hemolymph derives partly from the median branches of the cephalic aorta which curve dorsal and ventral to the brain (Fig. 2) and are seen in adjacent sections to communicate with the hemocoelic spaces anteriorly. Contributions of hemolymph also apparently derive via the antennules. The hemolymph is drained via spaces dorsal and lateral to the protocerebrum (Figs. 2 - 4).

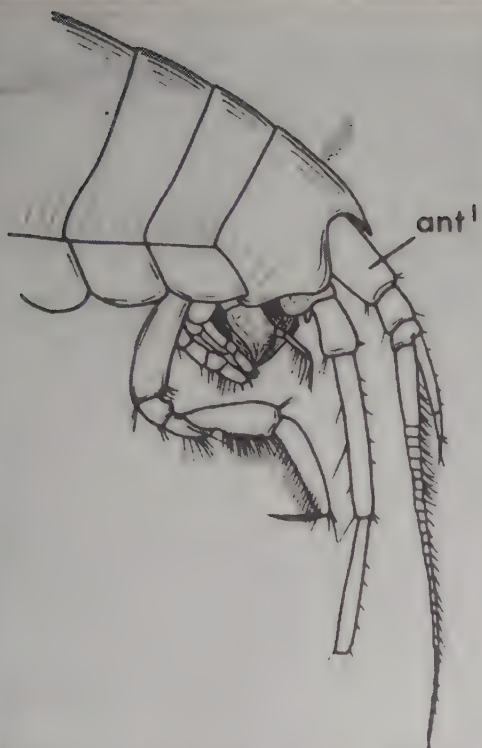
Fig. 1 Lateral view of head region. ant - antennula. After Sars (1895).

Fig. 2 Sagittal section of head region. The position of the antennula and part of the head cuticle are recognized from Fig. 1. ant - antennula; aor - aorta; epi - epidermis; nob - nerve from the organ of Bellonci; ob - organ of Bellonci; prc - protocerebrum. Gomori.

Fig. 3, 4 Consecutive horizontal sections through the brain and organ of Bellonci. cut - cuticle; ne - neurone perikarya; nob - nerve of the organ of Bellonci; x - acidophilic material in the cavities. Azan.

Fig. 5 Sagittal section. The perikarya of the neurones (ne) give rise to curving dendrites (arrows). The nerve from the organ of Bellonci (nob) passes out of the section in the area indicated by arrowheads. cut - cuticle. Gomori.

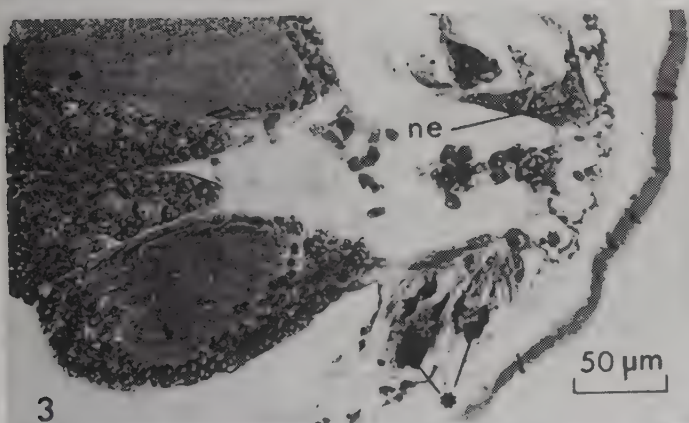
Fig. 6 Sagittal section. The fibres of the nerve are seen to the left of the arrow. broken circle - region of the cavities with dendrites; cut - cuticle; ne - neurone perikarya; pen - nucleus of a perineural cell; prc - protocerebrum. Bodian.



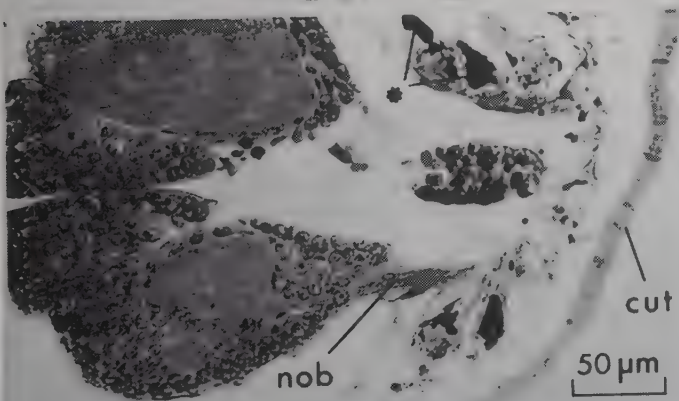
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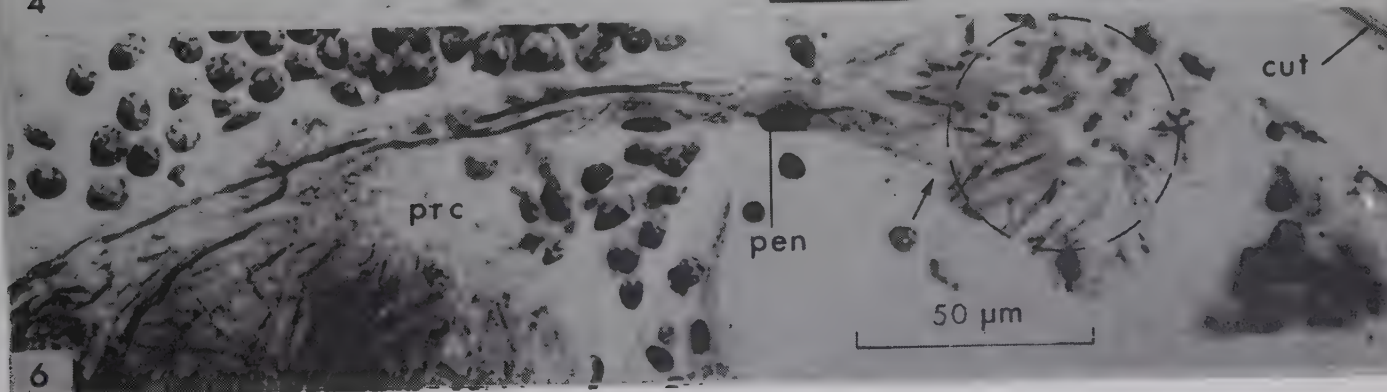
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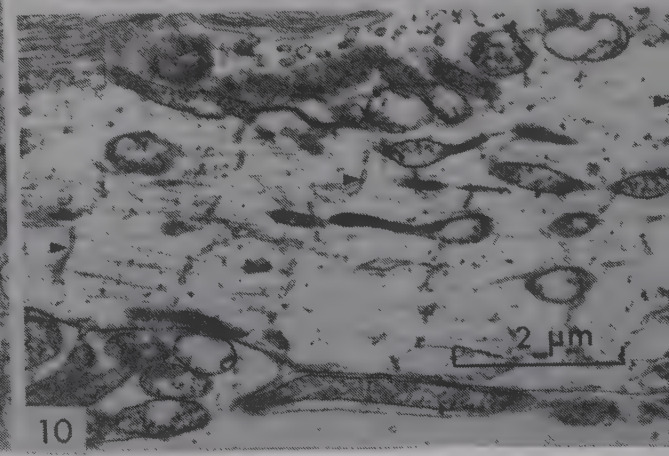
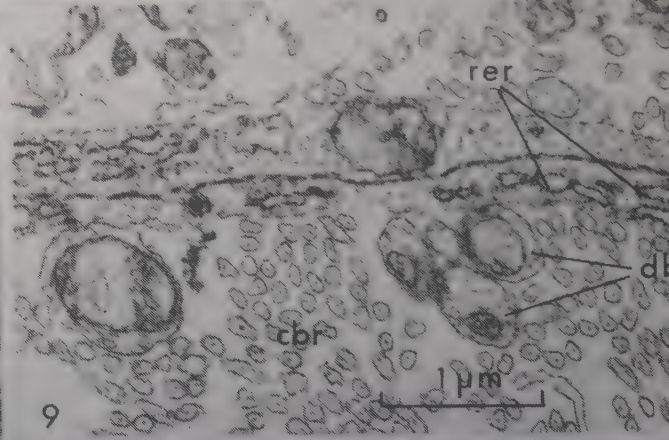
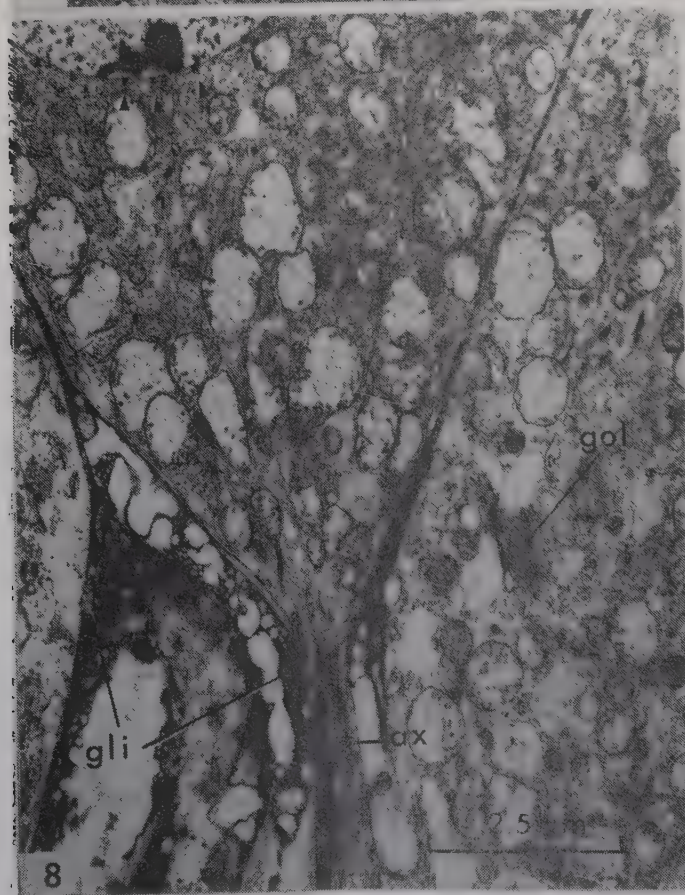
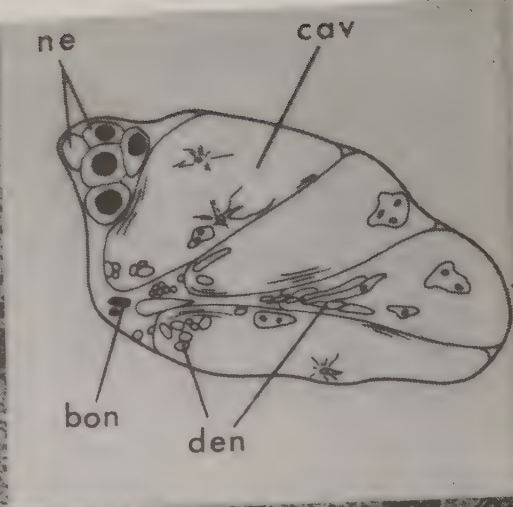
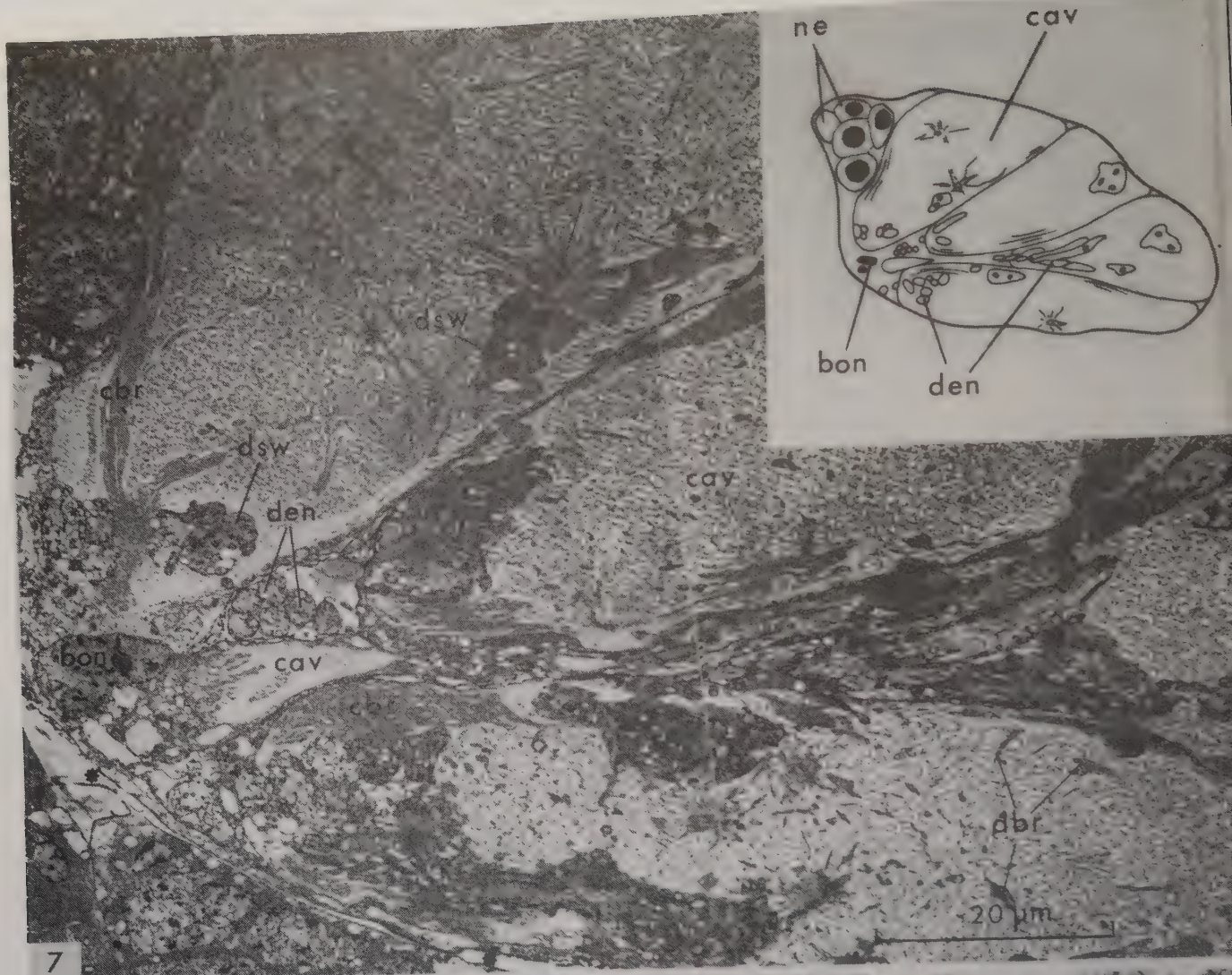
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3.2 Electron microscopical observations

The fine structure of the oB is presented in low power in Fig. 7. The outline of the organ and many of the structures from the light microscope are recognized here and from the diagram of the entire section (Fig. 7: inset).

The perineurium encloses the interior of the organ, where the sensory neurone perikarya and the neurites are found medially with the perikarya in an anterior position to the neurites. In this area a further cell type is found, which is referred to as glia.

The organ units lie laterally, comprising a thin wall of bordering cells and a central lumen with an apparently liquid matrix in which the dendrites and their cilia become suspended. A unit might reach 100 μm in length and up to 50 μm in diameter. Its walls appose the perineurium or the walls of adjoining units. Medially it borders to the neurite area.

In order to find the orientation relative to the animal, the diagram (Fig. 7: inset) may be compared to the sections represented in Figs. 3, 4.

3.2.1 The perineurium is built of lamellar processes from perineural cells. Only a few of these cells are found and their processes are confined to the surface layer of the organ. A basal lamina is formed towards the hemocoelic spaces and otherwise the perineurium is continuous with the connective tissue, present outside the organ. In the processes of the perineural cells bundles of microtubuli occur.

3.2.2 The glia cells are found in the antero-medial part of the organ. The ramifications of the cells surround the perikarya of the sensory neurones, the axons, the dendrites, and are found in the nerve from the organ. Between the neurites and especially between the axons, where glia processes frequently are found along both of two adjacent nervous elements, intercellular spaces occur, while between the neurone perikarya these spaces usually are lacking. In places where such interstitial spaces occur the glia elements are accompanied by a fibrillar material. This fibrillar material consists of fine filaments. The neurone elements are not always completely covered by glia as adjacent glial processes might leave gaps between them.

Fig. 7 Electron micrograph of horizontal section. bon - bordering cell nucleus; cav - cavity with granular material; cbr - ciliary branches; den - dendrites; dbr - dendritic branches; dis - distended ciliary shaft; dsw - dendritic swelling; ne - neurone perikarya; * - haemocoelic spaces. Inset: diagram of the section through the entire organ.

Fig. 8 Neurone perikarya. gol - golgi body in tangential section. ax - axon with microtubules; gli - glia; arrowheads - nucleal pores.

Fig. 9 Section through two bordering cell processes between cavities. cbr - ciliary branches; dbr - dendritic branches; rer - rough endoplasmic reticulum.

Fig. 10 Longitudinal section through dendrite. Clubshaped mitochondria and transversely arranged cisternae (arrows) are seen.

The glial cells have dark-staining cytoplasm and an elongate nucleus $10\text{ }\mu\text{m}$ in length or more. Numerous nucleal pores are seen in some nuclei, but their number varies between individual cells observed. The perikarya are scarce in cytoplasm.

3.2.3 The sensory neurones are bipolar with the perikarya organized into one unicellular layer, which is apposed to the perineurium dorsally, anteriorly and ventrally. Between the dorsal and ventral parts of this folded layer a narrow space is formed. Through this space the neurites leave the perikarya quite close to one another in a posterior direction with the axons medially and the dendrites laterally.

The shape of the perikarya is rounded to polygonal and their size is generally 15 by $20\text{ }\mu\text{m}$. The nucleus has a diameter of $10 - 12\text{ }\mu\text{m}$ and is less electrondense than the nuclei of neurones in adjacent regions of the protocerebrum, or those of the glial cells. Numerous nucleal pores may penetrate the distinct nucleal membrane of some of the neurones (Fig. 8). The cytoplasm of the neurone perikarya has mitochondria of an electronlucent, slightly swollen appearance, the few cristae belonging to the tubular type. Microtubules and endoplasmic reticulum are found along with ribosomes, which only rarely are carried on the cisternal membranes of the reticulum. Golgi bodies are present and close to these small granules of 50 nm diameter. The granules have membranes and generally are electronoptically empty, but granules with electrondense contents are found in small numbers scattered in the cytoplasm.

The axons (Fig. 8) have microtubules, neurofilaments and electrondense membranebound granules of 50 nm diameter. Areas of axo-axonal contact have not been observed. Instead the spaces between axons often are occupied by more than one glia process with interstitial spaces and accompanying fibrillar material. Axon diameters range between 0.2 and $1\text{ }\mu\text{m}$.

The dendrites cover the distance of about $60\text{ }\mu\text{m}$ between the perikarya and the organ units in one large bundle, which successively is divided into smaller groups towards the individual units. (The part of the dendrites found inside the units will be described along with the organ units below.) In the bundles the dendrites apparently are both held together and isolated from each other by glia elements. Close to the organ units the groups of dendrites are split further and often the dendrites enter the cavities singly. Each dendrite is then surrounded by a sheath of glial processes, which might be arranged into two concentric layers. The space left between these layers often contains fibrillar material. This space is obliterated when the glia is replaced by the bordering cells of the cavity wall (Fig. 11). The glia processes have a thickness of about $0.1\text{ }\mu\text{m}$. The dendrite diameter varies between $1 - 5\text{ }\mu\text{m}$ (Fig. 10), but the largest diameters, between $3 - 5\text{ }\mu\text{m}$, are found only inside the cavities of the organ units. In the cytoplasm numerous longitudinal microtubules are found with a diameter of 20 nm approximately. The mitochondria often taper into slender processes which give them the appearance of clubs. Occasionally electronoptically empty, membranebound profiles are found, apparently belonging to a sparse reticulum of the vesicular type.

In a few instances dendro-dendritic contact areas have been found, but without any apparent structures indicative of synaptic activity.

3.2.4 The bordering cells. The organ units have walls made up from processes of bordering cells. These cells have perikarya with little cytoplasm and their processes form lamellae in the range of $0.1 - 1 \mu\text{m}$ when surrounding the cavities. A wall between two cavities is built of two bordering cell processes but further processes might be included exceptionally. The membranes of apposed bordering cells appear electronoptically denser than do the membranes exposed to the cavity contents. The electrondense material appears to lie intercellularly (Fig. 9). The cytoplasm of the bordering cells has rough endoplasmic reticulum and a fibrillar material arranged into bundles traversing through the cell processes. Also groups of parallel microtubules are found in the bordering cells. Short processes from the bordering cells might enter the cavity lumen, but generally the walls of the cavities appear smooth.

3.2.5 The lumen of the organ cavity. Apart from the apparently liquid matrix fibrillar and granular material is found in the cavity lumen. The fibrillar material has fine filaments and is found close to cellular elements (Figs. 11, 12). Of the two granular materials one has an irregular structure and is found generally in the cavity. This material appears to be excluded from the immediate vicinity of the respective cell membranes by the finely fibrillar material. The second type of granules is found more rarely. These granules are spherical and roughly 100 nm in diameter (Fig. 17).

3.2.6 The dendrites. The cavities of the organ units are entered by the dendrites through the bordering cell layer. The dendrites might reach halfway or more into a cavity. The glia is not accompanying the dendrites into the cavities, nor do bordering cells enter with the dendrites, but a fibrillar material often is present close to the dendrite membrane. Terminally quite important swellings are found measuring about $8 \mu\text{m}$ (Figs. 7, 14). Also from the dendrites cilia arise.

In the cytoplasm of the larger dendritic profiles, $2.5 \mu\text{m}$ or more in diameter, there is found a system of transversely arranged cisternae (Fig. 10). Occasionally longitudinal elements connect to these cisternae and close to the dendritic membrane longitudinal profiles are found to communicate with the transverse system. There have not been observed any communications between this system and the extracellular space.

From the dendritic stems slender ramifications arise, $0.2 - 1 \mu\text{m}$ in diameter. These carry no swellings terminally and no cilia arise from them. The number of profiles of these ramifications may be quite large, as compared to that of the dendritic stems (Fig. 9). The profiles of the stems frequently are found close to the cavity walls, while those of the dendritic ramifications are randomly distributed.

Apart from profiles of dendrite stems and ramifications there are found in the cavity lumen a few profiles with a diameter similar to that of the dendritic ramifications but with a content of electrondense granules approximately 60 nm across.

3.2.7 The cilia are carried on the dendrite stems either terminally, emerging from the swelling, or laterally, emerging from the side of the dendrite. It has not been possible to ascertain if the cilia arise exclusively in pairs. Indeed there apparently are situations where single cilia arise.

The cilia have basal bodies with rootlets (Fig. 14) and a short neck region, while the rest of the ciliary shaft is distended into a more or less conical structure with the base of the cone facing into the cavity (Fig. 13). The basal bodies in the oB of *H. abyssi* appear to widen distally (Fig. 12 and 14, the pair of intensely electrondense strands). Material, denser than the surrounding cytoplasm, is found close to the basal body laterally and proximally. Also centrally in the basal body and between the basal body and the ciliary neck further electrondense material is found. Microtubules and membranebound electronlucent granules of approximately 60 nm in diameter are additional structures found close to the basal bodies. The rootlets have a transverse periodicity of ca 70 nm. The neck region is characterized here as the region where the ciliary shaft has an axoneme of the 9+0 type. In *H. abyssi* this region is slightly conical with the ciliary membrane smooth without folds or ramifications. The nine peripheral elements of the axoneme are here present close to the membrane, where electrondense material is concentrated at intervals of approximately 35 nm along each axoneme component and between the component and the membrane (Fig. 14). Basally the axoneme is continuous with the elements of the basal body.

The remainder of the ciliary shaft also is more or less conical, with a length of a few micrometers. This region has numerous microtubules at a random arrangement (fig. 13, 14). Electrondense granular material and membranebound electronlucent granules of ca 60 nm in diameter are found.

Fig. 11 A dendrite (den) penetrates into a cavity from the left. boc - bordering cell; cbr - ciliary branches; gfr - fibrillar material associated with glial cells; gli - glial cell processes; * - fibrillar material in the cavity.

Fig. 12 A dendrite with a cilium. arrows - neck region of cilium; den - dendrite; dis - distended ciliary shaft; grm - granular material; * - fibrillar material in the cavity.

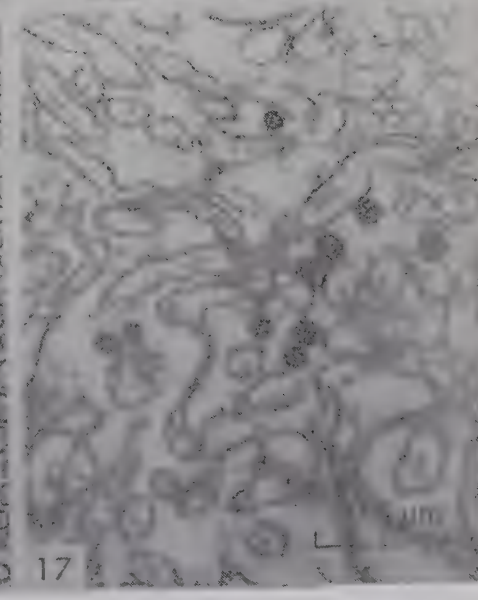
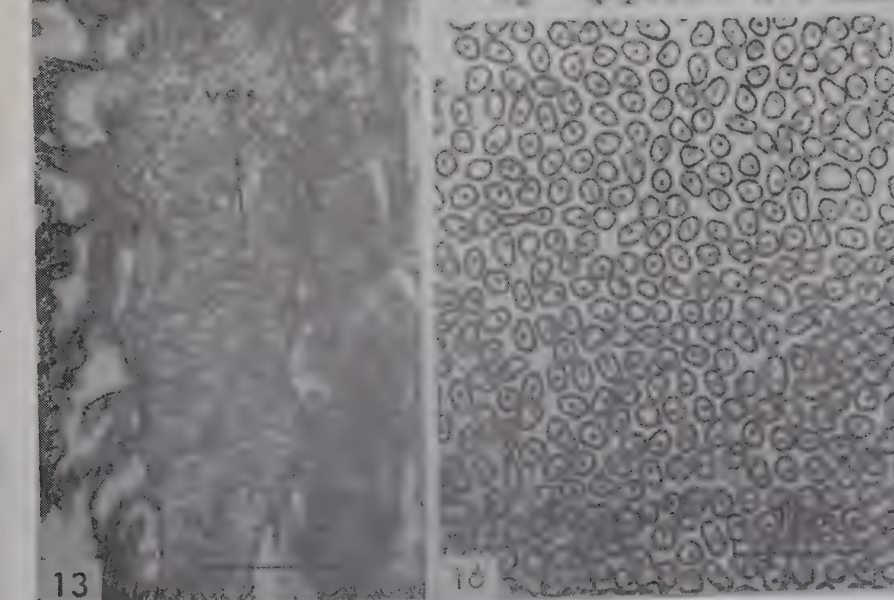
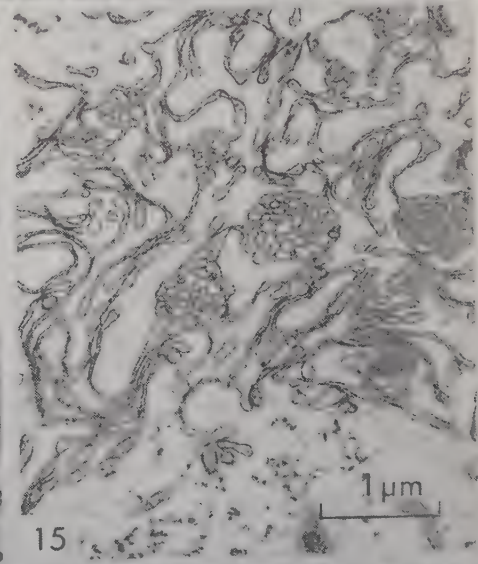
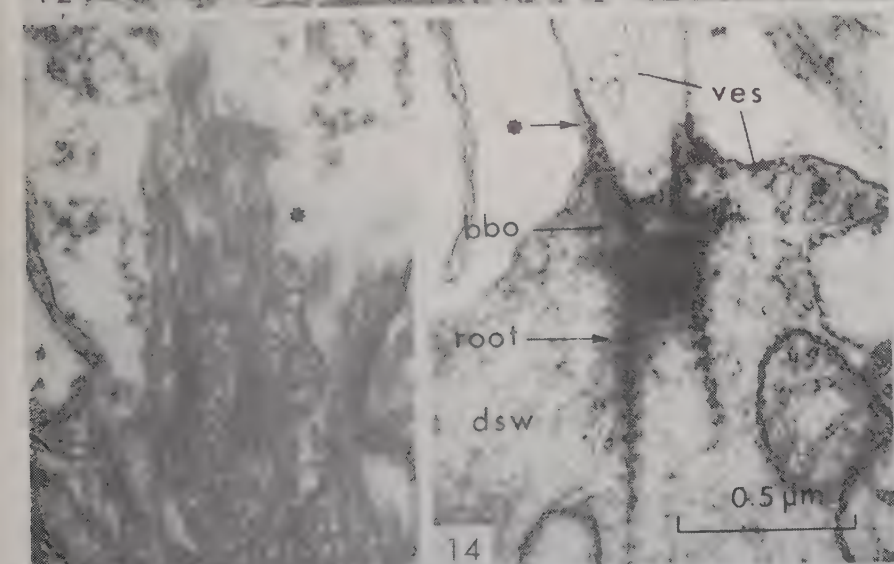
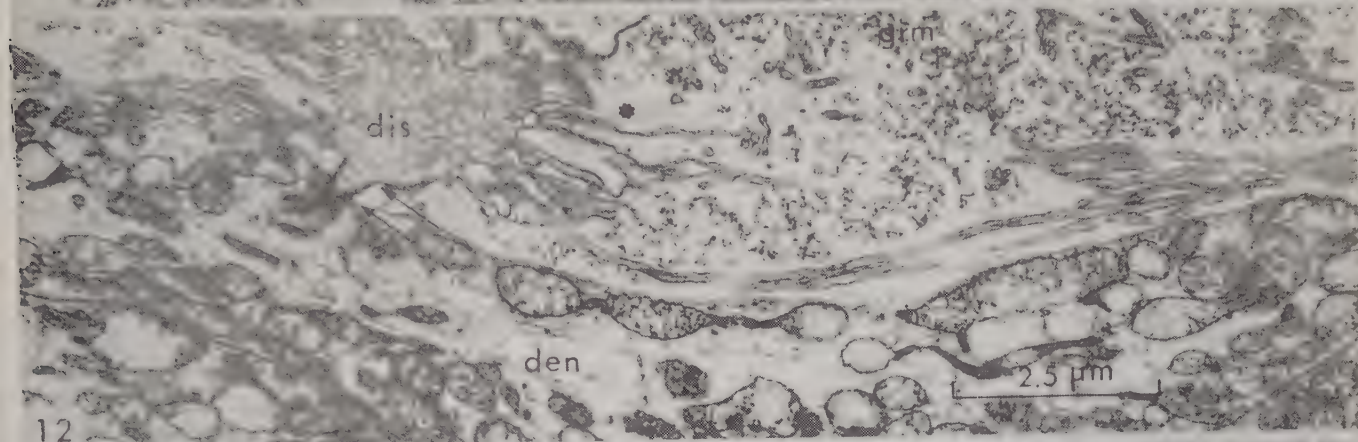
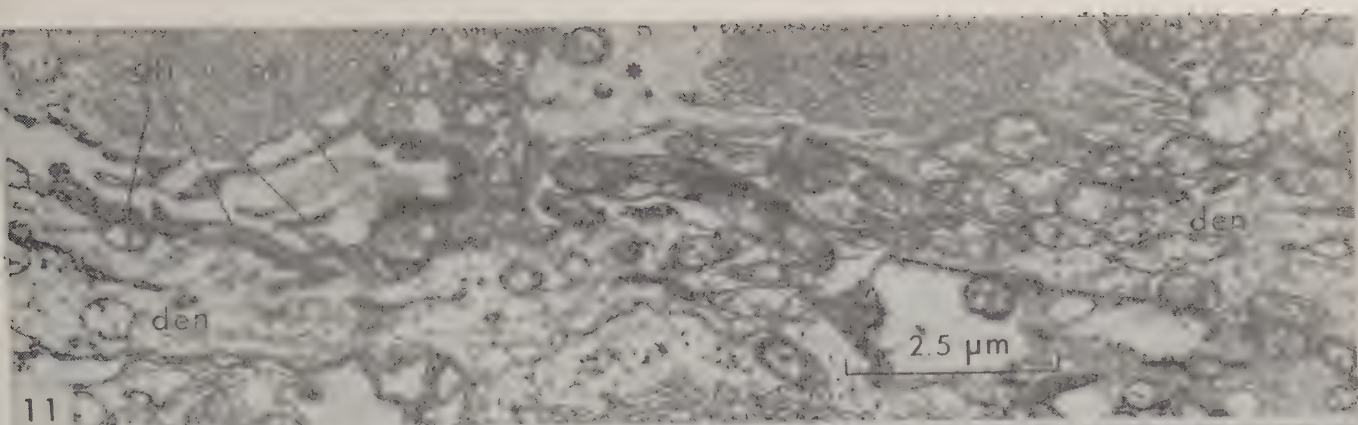
Fig. 13 Distended part of ciliary shaft with microtubules and branches. Several branches on the right are distended proximally to accomodate vesicles (ves). To the lower right lies a profile of a fibre with electrondense granules. * - fibrillar material in the cavity.

Fig. 14 Basal part of cilium with basal body (bbo) and rootlets (root). dsw - dendritic swelling; ves - vesicles; * - electrondense material between axoneme and ciliary membrane.

Fig. 15 Flattened ciliary branches in cross section close to a distended ciliary shaft. Vesicles are found inside distended parts of the branches.

Fig. 16 Area with ciliary branches. To the lower left a few branches are sectioned transversely.

Fig. 17 Ciliary branches with interspersed electrondense granules.



A large number of ciliary ramifications of a predominantly tubular cross section is carried on this part of the ciliary shaft. The smaller of these ramifications have one microtubule from the start but thicker ramifications with a few microtubules are also found. The latter soon ramify into branches with only one microtubule centrally. These final branches have diameters of 90 - 180 nm (Fig. 12, 16). Bundles of tubular branches 25 μ m in length have been observed. Close to the ciliary shaft the ramifications may be distended and sometimes flattened. In the distensions are found electronlucent granules, bound by a membrane and with diameters ranging between 50 - 120 nm (Fig. 13, 15).

4. Discussion

The organ of Bellonci in Halice abyssi is characteristically situated in the frontal region of the head, antero-dorsal to the brain. The position relative to the axis of the central nervous system, however, is an antero-ventral one, as the brain is tilted in a dorsal direction (cf Dahl, 1956).

The oB shows characteristic features regarding shape, number of units and distribution of sensory neurone perikarya. The spindle-shape appears to be characteristic of several oB among the Amphipoda, and is brought about by the perineural elements with additional strength probably contributed by the bordering cells with their contents of microtubules and bundled fibrillar material. Also the electrodense material found between adjacent bordering cells might indicate a kind of junctional structure, adding to the rigidity of the organ.

The postero-lateral, tapering structure of the oB certainly corresponds to that earlier described as a duct communicating with the exterior. The interpretation of the oB as a statocyst or a glandular organ, by earlier authors, certainly was encouraged by this conception of ducts. As shown here, the tapering parts of the organ appear solid and it has not yet been possible to demonstrate the presence of an external pore. If this is the case their function might be to stabilize the organ mechanically by anchoring it to the integument.

The partition of the organ in H.abyssi into about five organ units, each with a central lumen, is recorded for the first time among the Amphipoda. The finding of five hard coagula in the organ of Gammarus (Thore, 1932) might indicate that also this species has a subdivided organ. Thus a wider occurrence of subdivision of the oB among the Amphipoda could be expected. Also in the Mysidacea a subdivision into units is found (Kauri and Dahl, 1975), but the existing descriptions of multipartite organs among the Mysidacea do not show the nearly parallel arrangement of the units which characterizes the organ in H.abyssi.

Also the concentration of the neurone perikarya into one group is reminiscent of the arrangement in Boreomysis (Kauri and Dahl, 1975) and contrasts with that found among the Isopoda (eg Chaigneau, 1971) where perikarya may be found to be more evenly distributed throughout the organ wall. It follows that the dendrites in the organ of eg H.abyssi must have a greater length, than those in the isopods. The organization of the neurone perikarya into a unicellular layer, bent around the anterior part of the neurite region, is reminiscent of the organization in B. arctica, where an aggregation of neurites was observed in the centre of the group of neurone perikarya and close the organ cavity. Such an arrangement might prove advantageous regarding the trophic relations of the perikarya, bringing them within a short distance of the perineurium.

A characteristic of the neurite area, posterior to the neurone perikarya, is the glial element. This contributes to the spatial separation of especially the individual axons. The rather wide spaces found here might represent the necessary spaces for diffusion of metabolites in either direction between the neurites and the perineural cells, bordering to the haemocoel. The fibrillar material that accompanies the glial processes apparently partakes in the maintenance of the extracellular space between individual cellular processes.

The innervation of the oB characteristically is derived from the medulla terminalis. In the blind H. abyssi the innervation is comparable to that of Gammarus locusta (cf Thore, 1932; Elofsson, 1965) and Eurythenes gryllus. As the axons from the oB are difficult to trace deeper into the central nervous system, it has not been possible to identify the centre to which the tractus connects. The proximity to the optic tract, found eg in E. gryllus, might simply reflect the proximity of the organs distally, and must not necessarily imply close connections centrally.

The oB nerve appears to be entirely afferent, as those elements entering it from the organ, that have been observed, consist of axons from the sensory neurones. There are however the rare profiles in the organ cavities with contents of dense granules (60 nm ca), that are not directly comparable to the dendritic ramifications, why a small efferent component cannot entirely be excluded. A similar situation has been reported from the Mysidacea (Kauri and Dahl, 1975).

The axons and dendrites in the neurite area of the oB, apart from differences in location, have different dimensions. While the larger axons have diameters below one μm with an average of ca 0,6 μm , the dendrites measure from at least one μm and up to 3 μm . Direct apposition of one axon to another has not been observed, whereas dendro-dendritic appositions occur. This contrasts to those dendrites, individually invested in glial cells, as described from the oB in copepods (= 2. unit; Elofsson, 1971), but is comparable to the situation reported from the cirripeds (Walker, 1974; Kauri, MS). The rather small axon diameter is reminiscent of that found in the axons of Diastylis rathkei (Kauri, MS 2). Only the axons have been found to have the dense granules of 50 nm in diameter. The distribution of these granules in the neurone perikarya and in the axons indicates a possibility of an axonal transport.

The dendritic swellings in H. abyssi, though important, are not as conspicuously set off from the dendritic stems as eg those in B. arctica (Kauri and Dahl, 1975). The dendritic stems have diameters approaching those of the swellings and also carry cilia. Thus the entire dendritic stems in the organ cavity in H. abyssi might be considered as corresponding to the swellings in either species. The system of mainly transverse cisternae in the thicker dendritic stems is reminiscent of those found in the nerve cell processes of the protocephalic neurones in Doropygus seclusus. Also, in that species the cisternae apparently are found in the thicker profiles (Dudley, 1972; Fig. 22), which might indicate trophic functions involving eg mediation of metabolites. Similar transverse cisternae have been described from axons of photoreceptors (Dudley, 1965; Elofsson, 1966 b).

The ramifications from the dendritic stems contribute an additional area of dendritic membrane to the organ in H. abyssi. Similar ramifications have also been reported from B. arctica where they are more numerous, have larger dimensions and arise from the dendritic swellings.

It is unusual in the oB to find cilia arising along the dendrite as in H. abyssi. Moreover an arrangement of cilia into pairs appears not to be the rule in this species. The successive branching of the cilia is reminiscent of that in B. arctica, Anilocra (Chaigneau, 1972), and Balanus (Walker, 1974) and the flattened branches are also found in Anaspides (Kauri and Lake, 1972), Balanus (Walker, 1974) and B. arctica.

The concentration of electronlucent granules in distensions of the flattened ciliary branches is a feature also described from the oB in Carcinus maenas (Smith, 1974). The occurrence of similar structures in the distended cillum and in the region around the basal body in H. abyssi invites to speculations over a possible transport mechanism through the ciliary neck region for this material. It is however not possible to arrive at conclusions over the possible function of this material, its transport or the direction of such a transport from purely descriptive electron microscopy.

The three types of electrondense material found in the cavity are suspended in the apparently liquid contents of the oB cavity along with the dendritic and ciliary ramifications. The major electron dense component in the cavity is the irregularly granulated material. It is reminiscent of the granular material described from Sphaeroma serratum (Chaigneau, 1971). Its distribution is similar to that of the material reacting positively to the haematoxyline in the Gomori technique, and would then be comparable to the major electron dense material found in the organ cavity of B. arctica, although in the latter the material has a more regular configuration in the electron microscope. The finely fibrillar component that is found close to the dendritic and bordering cell membranes, is reported for the first time here. In the areas where it is present, it apparently excludes the irregularly granular material from access to the membrane surfaces mentioned. There is found no indication as to the mechanism of release of this material. The available cell processes are provided by the bordering cells, with a rather well developed granular reticulum, and the dendritic derivatives. The few profiles with contents of the dense granules of 60 nm in diameter would not be expected to partake in a release of larger amounts of material. The remaining electrondense material in the cavity comprises the rare granules of 100 nm in diameter. Secretory material of important dimensions, as reported from S. serratum (Chaigneau, 1971), has not been found in H. abyssi.

The staining characteristics of the oB in H. abyssi to the silver impregnation according to Bodian resemble those found in the organ of B. arctica. Apart from axones and dendrites, the basal parts of the ciliary shafts give a strong reaction. A weaker reaction is obtained in the distal, ramified parts of the cilia. Only the microtubular material shows a distribution along the cilia, that corresponds to the differences in staining intensity, why at least a part of the positive reaction to the silver stain should be located in the microtubules.

The oB among the Amphipoda has been considered to perform a diversity of functions, and has consequently been dedicated with various names, as mentioned introductorily.

The present examination of the oB in H. abyssi clearly demonstrates an oB of the type found generally among the Peracarida (Chaigneau, 1971, 1972; Kauri and Dahl, 1975). This confirms the comparison with the oB, that was made from light microscopical material (Dahl, 1963; Elofsson, 1965, 1966). More recently a paired organ was described from an anterior position to the brain in Rivulogammarus syriacus (Baid and Dabbagh, 1972, 1974). The organ is interpreted as a frontal organ, but, as mentioned introductorily, frontal organs are absent in the Amphipoda (Elofsson, 1965). The description given of the organ is rather brief, but the location, innervation and the structural characteristics given coincide with known characteristics of the oB. It is therefore suggested to regard this organ in R. syriacus as an oB.

Another organ has been described from a position ventral to the primary optic centra in a number of Amphipoda (Gabe, 1954, 1966), and mainly on histochemical ground interpreted as an oB. However, among the species examined were also those belonging to Rivulogammarus and Gammarus in which genera the oB is shown to have an anterior position to the protocerebrum. Because of this the organ clearly cannot be an oB and an interpretation of its nature must await a further examination of the innervation and the structural elements. The oB in H. abyssi, with its spindle-shape and with the dendrites always entering the organ units from the antero-median pole, shows a plan of organization more definite than is usually found in the organs of the Isopoda (Chaigneau, 1971, 1972) and Mysidacea (Kauri and Dahl, 1975). This type of organ is also found in Gammarus, while the organ in Eurythenes shows differences. It has not been the purpose of the present paper to discuss the variation of the oB among the Amphipoda, but it is apparent from earlier descriptions, mentioned introductorily, that a rather wide variation is to be expected.

The oB in H. abyssi appears to be a sensory organ, as judged from the ultra-structure of its neurones. The only indication of a possible neurosecretory activity is given by the dense, membrarebound granules of the perikarya and axons. Somewhat similar granular material has been reported from the neurones in the cavity organ in Artemia (Elofsson and Lake, 1971) and in the cavity organ and oB of calanoid copepods (Elofsson, 1971), where the granular material is made up by dense core vesicles. These vesicles are somewhat larger in size than those granules found in the neurones of H. abyssi, which less clearly show the dense core type. A combination of sensory and secretory, probably neurosecretory, functions seems probable (Chaigneau, 1972). The sensory functions, that might be performed by the oB, have been discussed repeatedly. Among these possibilities those of chemo- or photoreception are two of the more important. Here will be referred only to one paper regarding the Peracarida Isopoda, which have an oB similar to the one in H. abyssi (Chaigneau, 1974).

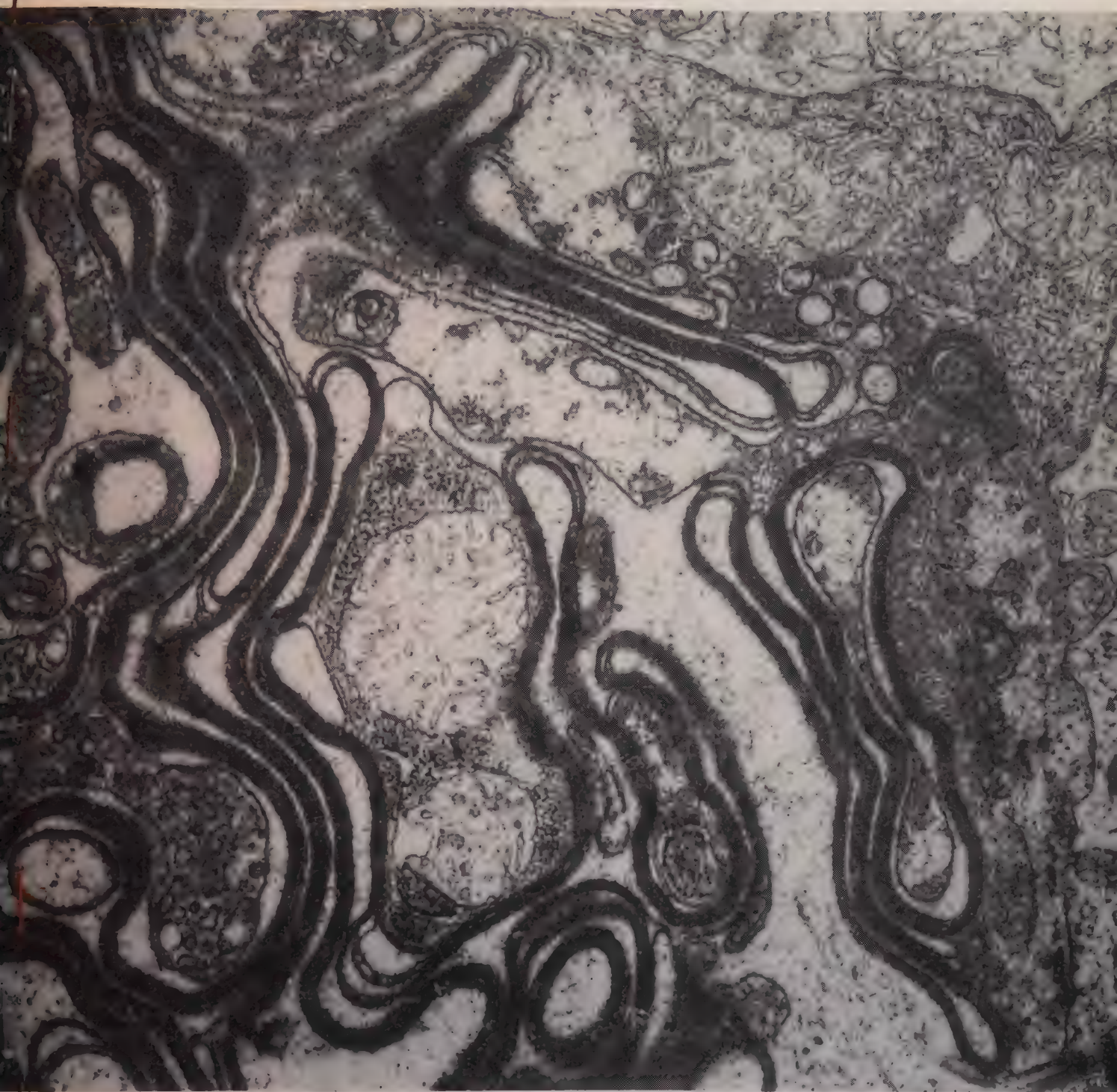
References

- Amar, R. 1950. Les formations endocrines cérébrales des Isopodes marins. C.R. Acad. Sci. Paris. 230:407-409.
- Baid, I.C., Dabbagh, S.A. 1972. On the neurosecretory system of Rivulogammarus syriacus Chevreux. Biol. Bull., 142:370-384.
- , —. 1974. Frontal organs in Rivulogammarus syriacus Chevreux. Curr. Sci. 43:551-552.
- Carlisle, D.B., Passano, L.M. 1953. The X-organ of Crustacea. Nature. 171:1070-1071.
- Chaigneau, J. 1971. L'organe de Bellonci du Crustacé Isopode Sphaeroma serratum (Fabricius). Ultrastructure et signification. Z. Zellforsch. 112:166-187.
- , —. 1972. Particularités ultrastructurales de l'organe de Bellonci d'Anilocra frontalis Milne Edwards, Crustacé Isopode Flabellifère Cymothoide. C.R. Acad. Sci. Paris. 274:1194-1197.
- , —. 1974. Evolution ultrastructurale en relation avec l'état sexual, de l'organe de Bellonci autochtone et implanté, chez le Crustacé, Isopode hermaphrodite, Anilocra frontalis. C.R. Acad. Sci. Paris. 279:771-774.
- Claus, C. 1887. Die Platysceliden. Alfred Hölder, K.K. Hof- und Universitäts-Buchhändler. Wien.
- Dahl, C. 1972. Preparation of Alcohol-Preserved Larvae of Culicidae (Diptera) for Scanning Electron Microscopy. Ent. scand. 3:181-188.
- Dahl, E. 1956. On the differentiation of the topography of the crustacean head. Acta Zool. 37:123-192.
- , —. 1963. Main evolutionary lines among recent Crustacea. In: Phylogeny and evolution of Crustacea. Museum of Comparative Zoology, Special Publ. Ed. H.B. Whittington and W.D.I. Rolfe. 1-26.
- Della Valle, A. 1893. Gammarini del Golfo di Napoli. Fauna u. Flora Neapel. 20.
- Dudley, P.L. 1969. The fine structure and development of the nauplius eye of the copepod Doropygus seclusus Illg. Cellule. 68:7-42.
- , —. 1972. The Fine Structure of a Cephalic Sensory Receptor in the Copepod Doropygus seclusus Illg (Crustacea: Copepoda: Notodelphyidae). J. Morph. 138:407-432.
- Elofsson, R. 1963. The nauplius eye and frontal organs in Decapoda (Crustacea). Sarsia. 12:1-68.

- Elofsson, R. 1965. The nauplius eye and frontal organs in Malacostraca (Crustacea). *Sarsia*. 19:1-54.
- . 1966. The nauplius eye and frontal organs in the non-Malacostraca (Crustacea). *Sarsia*. 25:1-128.
- . 1966 b. Some aspects of the fine structure of the nauplius eye of Pandalus borealis (Crustacea: Decapoda). *Acta Univ. Lund.* (II)1966(28):1-16.
- . 1971. The Ultrastructure of a Chemoreceptor Organ in the Head of Copepod Crustaceans. *Acta. Zool.* 52:299-315.
- ., Lake, P.S. 1971. On the Cavity Receptor Organ (X-Organ or Organ of Bellonci) of Artemia salina (Crustacea; Anostraca). *Z. Zellforsch.* 121:319-326.
- Gabe, M. 1954. La neurosécrétion chez les Invertébrés. *L'Année biol.* (Ser. 3.) 30:5-62.
- . 1966. Neurosecretion. Pergamon Press. Oxford.
- Gamroth, A. 1878. Beiträge zur Kenntnis der Naturgeschichte der Caprellen. *Z. wiss. Zool.* 31:100-123.
- Gomori, G. 1941. Observations with differential stains on human islets of Langerhans. *Am. J. Path.* 17:395-406.
- Gräber, H. 1933. Über die Gehirne der Amphipoden und Isopoden. *Z. Morphol. ökol. Tiere.* 26:334-371.
- Hanström, B. 1947. The brain, the sense organs and the incretory organs of the head in the Crustacea Malacostraca. *Acta Univ. Lund., N.F.* 58 (9):1-45.
- Kauri, T. MS. The fine structure of the organ of Bellonci in the Crustacea Maxillopoda, especially Balanus improvisus Darwin (Maxillopoda Cirripeda) and Derocheilocaris remanei Delamare and Chappuis (Maxillopoda Mystacocarida).
- . MS 2. The fine structure of the organ of Bellonci in Diastylis rethkei Kr. (Crustacea, Peracarida Cumacea).
- ., Dahl, E. 1975. Fine Structure of the Organ of Bellonci (SPX) in Boreomysis arctica (Krøyer) (Crustacea, Mysidacea). *Zool. Scr.* 4:41-47.
- ., Lake, P.S. 1972. The Structure of the Organ of Bellonci of the Syncarid Crustacean, Anaspides tasmanie (Thomson). *Z. Zellforsch.* 132:431-450.
- Knowles, F.G.W., Carlisle, D.B. 1956. Endocrine control in the Crustacea. *Biol. Rev.* 31:396-473.

- Langenbuch, R. 1928. Über die Statocysten einiger Crustaceen. Zool. Jb. Allg. Zool. 44:575-622.
- Mayer, P. 1882. Die Caprelliden des Golfes von Neapel. Fauna u. Flora Neapel. 6.
- Millonig, G.J. 1961. Advantages of a phosphate buffer for OsO_4 solutions in fixation. J. appl. Phys. 32:1637.
- Romeis, B. 1968. Mikroskopische Technik. R. Oldenbourg. München.
- Sars, G.O. 1895. An Account of the Crustacea of Norway. 1. Amphipoda. Christiania.
- Schmalz, H. 1914. Beiträge zur Kenntnis des Nerven- und Blutgefäßsystems von Lanceola, Vibilia, Rhabdosoma und Oxycephalus. Jena'sche Zeitschr. Naturwiss. 52:135-208.
- Smith, G. 1974. The Ultrastructure of the Organ of Bellonci of Carcinus maenas (Crustacea: Decapoda). Cell Tiss. Res. 155:127-134.
- Thore, S. 1932. Über Statocysten und Frontalorgane bei Gammarus pulex und Gammarus locusta. Zool. Jb. Anat. 55:489-504.
- Walker, G. 1974. The Fine Structure of the Frontal Filament Complex of Barnacle Larvae (Crustacea: Cirripedia). Cell Tiss. Res. 152:449-465.
- Zawadsky, K. 1915. Die Frontalorgane der Amphipoden. Zool. Anz. 45:65-73.

THE ORGAN OF BELLONCI



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LUND 1976

THE ORGAN OF BELLONCI

Summary: The Organ of Bellonci

The thesis comprises papers I - V,
presented separately.

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The papers

Summary: The organ of Bellonci. New information is introduced here from the Peracarida and Decapoda. Among the Peracarida a description of a superficial receptor of interesting relations comparatively, is presented, while the material from the Decapoda has interest regarding the interrelations between elements of the functional unit of the oB. The homologies of the oB complex and functional aspects of the oB unit are discussed here.

- I The fine structure of the organ of Bellonci in the Crustacea Maxillopoda, especially Balanus improvisus Darwin (Maxillopoda Cirripedia) and Derocheilocaris remanei Delamare and Chappuis (Maxillopoda Mystacocarida). - Kauri, T.

The structural characteristics of the oB complex among the Maxillopoda are presented and discussed comparatively. Observations on changes in the integumental elements during the moulting cycle are presented, and their significance for the structural elements of superficial receptors in the oB complex briefly discussed. The limited space available in the head of Derocheilocaris remanei, and its effect on the oB elements in this species are discussed.

- II The structure of the organ of Bellonci of the syncarid crustacean, Anaspides tasmaniae (Thomson). - Kauri, T. and Lake, P.S.

The oB among the Anaspidacea shows structural characteristics, intermediate between the two main types of the organ, found among the Maxillopoda-Peracarida and the remaining Malacostraca respectively. Characteristics of the innervation indicate a more complex connection of the oB complex centrally, than conceived previously.

The last three papers describe the oB among the Peracarida.

- III Fine structure of the organ of Bellonci (SPX) in Boreomysis arctica (Krøyer) (Crustacea, Mysidacea). - Kauri, T. and Dahl, E.

- IV The fine structure of the organ of Bellonci in Diastylis rathkei Kr (Crustacea, Peracarida, Cumacea). - Kauri, T.

- V Observations on the fine structure of the organ of Bellonci (SPX) in Halice abyssi BOECK (Crustacea, Peracarida, Amphipoda). - Dahl, E. and Kauri, T.

The Mysidacea and Amphipoda have an oB unit in several characteristics different from that found among the Cumacea-Isopoda.

A correlation between individual subtaxa and structural characteristics of the oB among the Mysidacea, is indicated.

An alternative significance is suggested for the intense reaction of the cavity contents to secretory stains, which previously has been attributed to neurosecretory material in the cavity.

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THE ORGAN OF BELLONCI

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Abstract

A presentation is given of the fine structural detail accumulated so far on the organ of Bellonci (oB) and related superficial receptors. New observations on the fine structure of these receptors from Maxillopoda, Anaspidacea, Peracarida, and Decapoda are presented. The oB comprises from one to several organ units. These are structurally identical within an individual organ, and contain the functional elements of the oB. These elements are analysed comparatively, and characteristics for receptor units on the deep (oB) level and on the superficial level are established. The homologies of the individual receptor levels and of the entire oB complex are discussed. Two homologous organ complexes are established as components of one homologous oB complex. The functional implications of the structural characteristics of the oB elements are discussed.

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Introduction

The organ of Bellonci (oB) is one of several cephalic receptors of the Crustacea. It shares an innervation from the medulla terminalis of the protocerebrum, or corresponding parts, with such superficial receptors as the sensory pore/papilla (eye papilla) (Hanström, 1947; Chaigneau, 1973 a, 1973 b) and the cavity receptor (Elofsson and Lake, 1971). A close association between the superficial receptors and the oB has long been recognized among the Malacostraca (cf Hanström, 1947 and Gabe, 1966). The recognition of the oB among the non-malacostracan taxa is of a more recent date (Dahl, 1963, 1965; Elofsson, 1966). The presence of superficial receptors, associated with the oB in the non-Malacostraca has been recognized (Kauri, 1966, I; Elofsson, 1971; Elofsson and Lake, 1971; Dudley, 1972; Walker, 1974).

The oB thus represents the deep components of a complex comprising both superficial receptors and deep receptors (Elofsson and Lake, 1971; Kauri, I). This complex is tentatively named the oB complex.

Apart from the oB complex and the compound eyes there is one more major complex of cephalic receptors comprising the frontal organs and nauplius eye. This organ complex derives its innervation from the nauplius eye centre in the protocerebrum, and comprises reduced and functioning photoreceptors. Earlier the concept of frontal organs comprised various elements, among others those belonging to the frontal organ-nauplius eye complex and those of the oB complex. So the sensory pore/papilla at the time of Hanström's survey of the oB (= X organ) and the sensory pore/papilla (= eye papilla) (Hanström, 1947), was considered a dorsal frontal organ. Clear distinctions were made here by Elofsson, investigating the frontal organ nauplius eye complex (Elofsson, 1963, 1965, 1966). The concept of the oB complex can be traced back to Bellonci, who depicted the organ in *Sphaeroma* (1881), indicating it with an X for unknown nature. It was this "X" that was honoured by Hanström (1931) by naming it the X organ. The further development of the oB nomenclature (including the synonyms X organ, PDX-pars distalis X organi, SPX-sensory pore/papilla X organ) has been extensively discussed by Gabe (1966) and the reader is referred to that paper for details. A short discussion of the functional implications of the term X organ is given by Kauri and Lake (1972/II/). The current term oB, is credited Amar (1950) and has been accepted by recent authors (eg Chaigneau, 1969; Jacques, 1969; Lake and Ong, 1972; Smith, 1974). The earliest descriptions of organs, later identified as oB include those of Claus (1863), Copepoda and Gamroth (1878), Amphipoda.

Elements of the oB complex have been identified from the Anostraca (Elofsson, 1966), Mystacocarida (Dahl and Elofsson in Elofsson, 1966; Kauri, I), Copepoda (Dahl, 1963; Elofsson, 1966), Cirripedia (Dahl, 1963; Kauri, 1966), Ascothoracica (Kauri, 1966), Decapoda (Hanström, 1931), Stomatopoda (Hanström, 1931), Anaspidacea (Hanström, 1934), Euphausiacea (cf Hanström, 1947), Mysidacea (Hanström, 1933), Cumacea (Ståhl, 1938), Tanaidacea (Gabe, 1966), Isopoda (Amar, 1950, 1951), Amphipoda (Dahl, 1963), and Leptostraca (Ståhl, 1938). Elements of the complex have not been reported from the Ostracoda, Cephalocarida, and Branchiura. In the Phyllopoda Notostraca an organ of uncertain affinities is reported as a probable candidate (Elofsson, 1966).

The oB

The oB is built up from one vesicular unit in the Maxillopoda (Kauri, I), Cumacea (Kauri, IV), and the Isopoda (eg Chaigneau, 1971a). In the Mysidacea the organ might comprise one unit as in eg Eucopia (Dohrn, 1906), two units as in Boreomysis (Kauri, unpubl.) or several units as in Mysis (Hogstad, 1969; cf Kauri and Dahl, 1975/III/). In the Amphipoda organs of several units are known so far (Dahl and Kauri, V). In the Anaspidacea (Kauri and Lake, 1972/II), Decapoda (Chaigneau, 1971b, 1973 a) (Fig. 1), Stomatopoda (Chaigneau, 1972 a), and Leptostraca (Chaigneau, 1973 b) several units are present, and in the Euphausiacea a closer examination is necessary to answer this question, as the walls of the units might be too thin for the resolution power of the light microscope. Generally the larger organs are subdivided, but while the single-unit organs among the Peracarida might approach a few hundred μm , that found in the Anaspidacea is subdivided into units of ca 16 μm diameter. Apart from having functional implications, the size, subdivision, and shape of the organ might have a systematic value. Thus among the Decapoda there exists a diversity in the oB morphology (Drach and Gabe, 1960), and among the Mysidacea there appears to be found a certain correlation between morphological variation and systematics (Kauri and Dahl, 1975/III/). However, the number of species investigated so far is too small to establish a pattern of systematic variation in most taxa.

Regarding the units of an organ, there are as yet no indications of a variation in the component elements between individual units, why the composite organs will be considered as built up from identical units.

The ob units. The oB might comprise elements from sensory neurones, supporting cells, and perilemmal cells.

The sensory neurones. Elements from these neurones are the only nervous elements that have been ascertained in the oB units so far with the exception of the profiles of uncertain affinities found eg in the Amphipoda (Dahl and Kauri, V). The neurones, where described, are found to be bipolar.

Only two cytoplasmic inclusions of the sensory neurones will be mentioned here. The presence of phaosomes is so far reported from the Decapoda (Lake and Ong, 1972; Chaigneau, 1975) with certainty. Structures that might be interpreted as phaosomes are also shown in Anilocra (Chaigneau, 1972 b), though not interpreted as such, why a conclusive diagnose must await confirmation. The phaosomes are considered indicative of photoreceptory activities in the cells possessing them (Dudley, 1969; Lake and Ong, 1972).

Dense core vesicles are reported from the Copepoda (Elofsson, 1971) and from Decapoda (Chaigneau, 1975). Membranebound granular material of similar dimensions has been reported from the neurone parikarya and axons from the Amphipoda (Dahl and Kauri, V) and Decapoda (Kauri unpubl.). No conclusions as to the nature and function of these vesicles can be made without further examination. The tests for biogenic amines (Elofsson, 1971) were reported negative, and it must be noted that the axones of only very few organs have been examined so far.

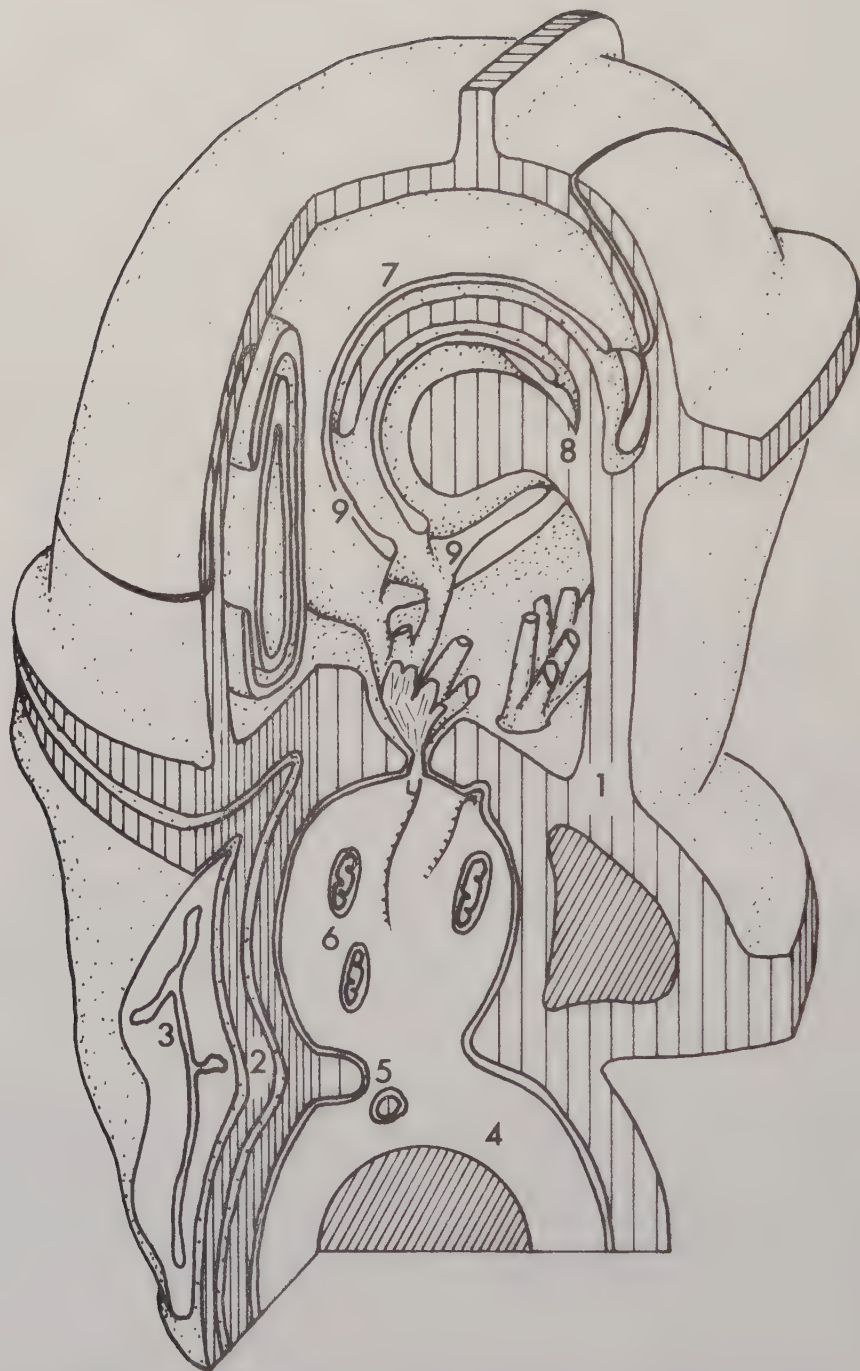


Fig 1 Diagrammatic representation of the oB unit. The bordering glia is hatched vertically (1), along with another glial cell to the left (2), where also a capillary is found (3). The sensory cell, with the perikaryon in the lower centre (4), has trophospongium (5), a constricted apical part with mitochondria (6), and a pair of cilia. The cilium to the left contributes to the onion body centrally in the organ unit (7), with two bordering glia processes (8) projecting inbetween the ciliary lamellae (9). Only two lamellae of the onion body are shown. The diagram is based on information from the oB units in Crangon and Leander. For clarity the dimensions of the individual elements are exaggerated and their numbers reduced.

The sensory perikarya might be located within the organ, as in the Peracarida (cf Chaigneau, 1971 a; Kauri and Dahl, 1975/III/), Decapoda (Chaigneau, 1971 b, 1975; Lake and Ong, 1972; Smith, 1974; Kauri, unpubl.), Stomatopoda (Chaigneau, 1972 a), and Leptostraca (Chaigneau, 1973 b). The perikarya are elongated in the Stomatopoda, Leptostraca, and in the Decapoda *Paratya* (Lake and Ong, 1972), *Troglocaris*, and *Atyaephyra* (Chaigneau, 1975) and often more or less constricted, forming a distal part usually with numerous mitochondria and a proximal perikaryon proper. In the Euphausiacea the neurone perikarya likewise appear to be located within the organ (cf Hanström, 1947).

The perikarya might also be located in the medulla terminalis or a corresponding part of the protocerebrum. This is the case in the Mystacocarida (Kauri, I), Copepoda (Elofsson, 1971; Dudley, 1972), and the Cirripedia (Walker, 1974; Kauri, I). In these organs dendrites are formed, connecting the perikarya with the organs. Dendrites are also formed from the neurones among the peracarideans belonging to the Mysidacea (Kauri and Dahl, 1975/III/), Cumacea (Kauri, IV), and Amphipoda (Dahl and Kauri, V). Also in the Anaspidacea the neurone perikarya are located outside the oB. They apparently lie in the layers of perikarya of the medulla terminalis and the medulla interna, with dendrites formed (Kauri and Lake, 1972/II/).

The dendrites, or where these are lacking, the terminal parts of the neurones, usually terminate in the wall of the organ units, penetrating the supporting cells to expose the areas of ciliary origin to the cavity. An exception from this situation is found among the Mysidacea (Kauri and Dahl, 1975/III/) and Amphipoda (Dahl and Kauri, V), where the dendrites penetrate further into the cavity. These dendrites (unsheathed) furthermore ramify in the cavity, exposing a larger area of dendritic membrane to the cavity contents (Fig. 2).

The amount of mitochondria, found close to the area of ciliary origin usually is large, as in the Decapoda (eg Chaigneau, 1971 b; Lake and Ong, 1972), or the Cirripedia (Walker, 1974; Kauri, I), but exceptions are found in the Cumacea (Kauri, IV) and are also noted from the Leptostraca (Chaigneau, 1973 b).

Generally one pair of cilia emerges from each neurone. Apart from the occasional exceptions, where only one cilium is reported (Lake and Ong, 1972; Chaigneau, 1975), the Copepoda present a unique situation with multiciliated neurones (Elofsson, 1971; Dudley, 1972).

The organ units usually have a large surface of ciliary membranes exposed to the cavity. This increase of ciliary membrane, however, might be brought about along one of the following ways in the individual species: (1) the number of dendrites in each organ might vary. The extremes are found among the Copepoda with one dendrite (Dudley, 1972) and in the Mysidacea with the number of dendrites approaching 50; (2) the number of cilia on each dendrite may vary. Here the extreme situation in the Copepoda with multiciliated dendrites has been mentioned above; (3) the extent of ramification in the individual cilia might vary. Here also the Copepoda present an extreme with unramified cilia (Dudley, 1972). The degree of ramification has not been quantified for the individual species examined, but an intermediate situation is found in the organ of the Anaspidacea (Kauri and Lake, 1972/II/) with moderate ramification of the cilia as compared to eg those of the Decapoda (Chaigneau, 1971 b).

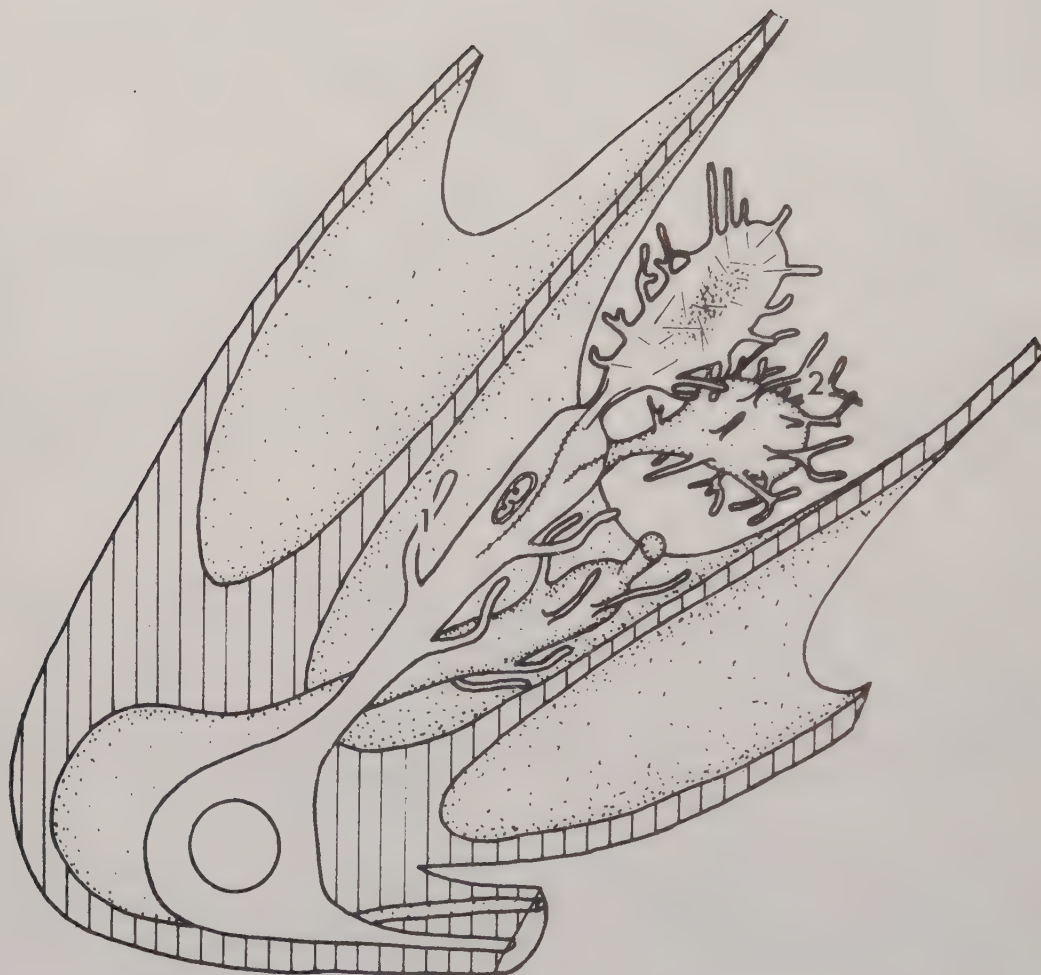


Fig 2 Diagrammatical representation of the oB in *Halice abyssii* (cf Dahl and Kauri, V). The proximal parts of three of the organ units are shown. Glial elements are shown vertically hatched. Only two neurones are represented. Note the ramification of the dendrites (1). The ciliary ramifications are drawn shortened for clarity; the terminal tubular branches are not represented (2).

Microtubules have been found to be present in cilia from all species where they have been sought for. Though no quantification has been made, the number of microtubules in the individual cilia appears to be roughly proportional to the surface area of the ciliary membrane. The amount of ciliary membrane and of microtubules apparently will have to vary during cyclic degradation of the ramifications (cf Gabe, 1966; Smith, 1974). Supposed variations in the number of ramifications in the Cirripedia (Kauri, I) also indicate a possible variation in the number of microtubules. A de novo formation of microtubules in the distended ciliary shafts is suggested (Kauri, I). In this connection it is interesting to speculate over the significance of the electrondense material repeatedly found in the ciliary shafts of the oB cilia (eg Dahl and Kauri, V). This material might represent a center of microtubule organization, an MTOC in the sense of Pickett-Heaps (1969) cf also Pitelka (1974).

There are two main types of ciliary ramification in the oB, the tubular and the lamellar types. The former, comprising the terminals of ca 100 nm diameter, is reported from the Maxillopoda (cf Kauri, I), Peracarida (eg Chaigneau, 1971a), Anaspidacea (Kauri and Lake, 1972/II/), and the Decapoda (Kauri, unpubl.). The lamellar type is reported from the Decapoda (Chaigneau, 1971 b), Anaspidacea (Kauri and Lake, 1972/II/), Stomatopoda (Chaigneau, 1972 a), and the Leptostraca (Chaigneau, 1973 b). Apart from occasional occurrence of lamellary configurations in species with a mainly lamellar ramification, the Anaspidacea are unique in having both types of ramification represented in the same organ unit. Another occasion where both types of ramification appear to be present is in the oB of Pandalus, though the 100 nm rami here are very rare and in bundles of a few rami. The habitual appearance of the Pandalus units is one, reminiscent of those in the anaspidacean organ (Pl 3 A). Units similar to those in Pandalus are reported by Chaigneau from another decapod Atyaephyra (1973 a). In both species these units are characteristically located in a delimited area of the organ. The characteristic organization of the lamellar branches into the onion-body configuration is also lacking in these organ units of the Decapoda, as they also are lacking from the anaspidacean organ. The one onion-body configuration reported from the Anaspidacea (Kauri and Lake, 1972/II/), was an misinterpretation of a cytoplasmic structure, somewhat similar to the phasomes. Thus, on the information presented so far, three types of ciliary configurations pertaining to individual oB units are found: (1) the tubular type, (2) the lamellar type with onion bodies, and (3) the tubular/lamellar type without onion bodies.

Vesiculation or tubulation of the lamellae in oB units have repeatedly been reported (Chaigneau, 1971 b; Lake and Ong, 1972; Smith, 1974). These observations have been verified on material from Leander adspersus and Crangon crangon (Kauri, unpubl.). The presence of vesicular material apparently in different stages of degradation indicates that this is a metabolic phenomenon and not brought about during processing due to fixation artefacts. However, the more distinct tubular and vesicular profiles, often observed inbetween the lamellar processes of the onion body, in some cases might represent such artefacts. It is difficult to explain the formation of both intralamellar and interlamellar vesicles in the same preparation (Pl 1 C, D) in other terms. At least one of these should represent an artefact. This phenomenon is notable in order to underline the need for extreme care while analysing the intra- or extracellular nature of membrane configurations found in the onion body. Occasionally also the vesiculation might involve two adjacent lamellae. The tubules resulting from the tubulation of lamellae should not be taken for tubular ciliary branches. A clear distinction can be made by analysing their content of microtubules, as the former profiles lack these.

The supporting cells. Under this term the cellular elements of the oB, other than the sensory and perilemmal elements are included. The supporting cells might be expected to be concerned with mechanical and trophic support to the organ units and the neuronal elements, why their character rather resembles that of glial cells. This concept has been indicated in some species by naming the cells accordingly. These cells might be found on two levels, those directly bordering to the organ cavity, and those located external to this layer. These two levels have been recognized in several species, regardless of systematic position (Chaigneau, 1971 a, 1973 b, 1975; Kauri and Lake, 1972/II/; Dahl and Kauri, V). The cells directly bordering to the cavity have been called bordering cells (Chaigneau, 1971 a), among the Peracarida, Bellonci glia (Kauri and Lake, 1972/II/), in the Anaspidacea and glial cells (Chaigneau, 1971 b, 1972 a, 1973 b; Elofsson, 1971) in the Decapoda, Stomatopoda, Leptostraca and Copepoda respectively. A number of authors also have used the term supporting cell (eg Dudley, 1972; Walker, 1974). It would appear that the term bordering glia might be a neutral term indicating the direct relation to the oB cavity. The cells in the external position, where reported, usually have been termed glia cells.

In the individual oB the development of the glial component shows wide variations. This apparently depends partly on the organ size and partly on the nature of its trophic demands. In the Mystacocarida (Kauri, I) only one cellular element, present in one layer of thin cell processes only, meets the entire functional demands placed on the organ wall, while in the larger oB of the Amphipoda (Dahl and Kauri, V) the glial elements specialize to meet individual demands on the two levels.

The bordering glia is of special interest in the oB. These cells, with few exceptions, show an electron dense cytoplasm and, in certain species, myeloid structures indicative of lytic activities (Chaigneau, 1971 a). In a few instances indications of phagocytic activity are found (eg Kauri, I). In the Decapoda trophic processes from the bordering glia are found to project into the sensory neurone perikarya (Pl 1 B). These processes constitute a trophospongium (cf short review by Scharrer, 1964). Also the bordering glia frequently is found to have processes between the lamellae of the onion bodies (Pl 2 A, B), as also is shown in Fig. 1. These processes often have mitochondria and ribosomes. The plasma membrane of these cells always is very thin in comparison with that of the sensory neurones (Pl 1 B) and also that of the ciliary membranes (Pl 2 A). This explains why it rarely is observed. Also this characteristic of the membrane might indicate higher contents of lytic enzymes, resulting in autolysis before fixation. A further indication of autolysis might be the electron dense homogenous cytoplasm often found in these cells (Pl 2 B). The glia process in Pl 2 B indicates a phagocytic process in these cells. The inclusions (1) probably represent phagocytic vacuoles with the membranes of the vacuoles autolyzed. The material, included in these vacuoles is similar to the vesicular material found free in the organ cavity on the upper left (cf Pl 2 A). The myeloid material (2) might represent older phagocytic vacuoles. The mitochondria and lysosomelike bodies found in the onion bodies of Paratya (Lake and Ong, 1972) most probably are contained in such glial processes. In the Mystacocarida, material of relatively low electron density is found scattered in the bordering glia. Also similar dense material is observed close to the membrane, with concentrations locally (Pl 2 C). This might indicate a release of material into the cavity. The significance of such observations is low however, and the observation is recorded only to illustrate one possible way of obtaining the granular material observed in the cavity.

It appears that the glia elements and the sensory neurones constitute a functional unit in the oB of close interrelations.

The perilemmal cells, found around the oB, are continuous with the perilemmal element of the oB nerves and protocerebrum. In the Mystacocarida (Kauri, I) this element is lacking, its functions apparently taken over by the single layer of glial cells in the organ wall. Also in the Anaspidacea the perilemma is lacking, the glial elements directly apposing to cells in the epidermis distally and being continuous with the glia of the ganglionic cell layers of the medulla terminalis and interna proximally. In the Amphipoda (Dahl and Kauri, V) the perilemmal layer is very thin, and in the Cumacea a multilayered perilemma has been observed (Kauri, IV). Frequently a basal lamella is formed on the external perilemmal surface, where this borders the haemocoel. It is not clear which cells form this lamella, but it might be formed by haemocytes (cf Neville, 1975).

Information regarding the perilemma in the larger organs among the Decapoda is lacking so far.

Additional elements however are present in the larger organs. In the Decapoda the oB is vascularized, with thin arteries penetrating the organ. Branches of such arteries are found close to the oB units (Pl 1 A). Along these arteries and along the bundles of nerve fibres cellular elements of glial nature as well as other elements are found. The nature of these latter elements has not been investigated. In the oB of Carcinus (Smith, 1974) reports two types of neurosecretory neurones in the interior of the oB.

The superficial receptors of the oB complex

A homology between the superficial receptors of the Maxillopoda, the cavity receptor in the Anostraca and the sensory pore/papilla among the Malacostraca based on structural information, known so far, has been tentatively suggested (Kauri, I). A similar homology is indicated by Chaigneau (1973 a), though not explicitly stated. The cautious approach to this homology problem is justified, as the information on the structural relationships of these organs still is restricted to only a few species, and often only to one single species, from the taxa examined.

Among the Malacostraca so far the fine structure has been examined from the Decapoda and Leptostraca (Chaigneau, 1973 a, 1973 b). Here a few preliminary results from an examination of the fine structure of the sensory pore/papilla in a number of crustaceans (Kauri and Myhrberg, unpubl.) will be presented concerning the sensory papilla in Boreomysis arctica of the Peracarida.

The sensory organ is restricted to the apical part of the papilla (Pl 3 B). A few pores are found in SEM, but the location of these appears to be inconsistent, when comparing individual specimens. Also a penetration of the cuticle has not been ascertained so far, but in the region covering the sensory organ, the cuticle is appreciably thinner. This is interpreted as an indication towards a chemoreceptor function. In sections parallel to the axis of the papilla and the receptor, a layer of epidermal cell processes is found under the cuticle (Pl 3 C). These processes carry microvillous structures, characteristic of epidermal cells in the arthropods (cf Neville, 1975).

Under this epidermal layer a cavity is found, enclosed by epidermal cells peripherally and sensory dendritic terminations along with glial elements proximally (Pl 3 D). The dendritic terminals are covered by the glial processes, except where the single pair of cilia originates.

The cilia have rootlets, basal bodies, a short neck region with an axoneme of the 9+0 type, and distally a distended shaft. From the latter tubular branches arise through irregular, successive branching. Microtubules are numerous in the ciliary shaft and a few are found in the profiles of the branches. Occasionally branches with a single microtubulus are found. Apart from ciliary branches also processes from epidermal cells are located in the organ cavity. The organ is sheathed by a perilemma, several cell layers deep. The neurone parikarya are located proximally, probably in the concentration of perikarya close to the proximal unit of the oB. The innervation is derived, along with that of the oB from the medulla terminalis. The morphology of this receptor is that of a sensory pore, similar to the main sensory pore, described from the Decapoda (Chaigneau, 1973 a). The organ in B. arctica represents a situation where a sensory pore is located apically on a papilla. The distinction between pore and papilla thus appears to be one of location of the sensory receptor morphologically rather than one involving special characteristics of the receptor itself, a situation which might be found more generally among the larger sensory papillae in crustaceans.

Notwithstanding the unbranched cilia in the cavity receptor of the Anostraca (Elofsson and Lake, 1971), the individual characteristics of the superficial receptors among the Maxillopoda (cf Kauri, I), and the orientation of the ciliary branches towards the penetrating cuticular pores in the Decapoda (Chaigneau, 1973 a), the elements of these superficial receptors and their interrelations are comparable. The individual differences regarding the epidermal components might be explained through different phases of the moulting cycle in the individual specimens examined, as discussed for the organ complex among the Maxillopoda (Kauri, I).

Probably the sensory pore in Nebalia (Chaigneau, 1973 b) will turn out to be comparable to the type of receptor discussed here, but further information on its structure is needed, especially regarding the peripheral component.

The suggestion made by Chaigneau (1973 a) of a probable homology of the lateral sensory pore of Atyaephyra with the first unit of the copepod sensory complex (Elofsson, 1971) is interesting. A conclusive homologization of course must await further information on the first unit in Copepoda.

A light microscopical observation on Caprella linearis (Kauri, unpubl.) of a small sensory pore, distal to the oB, and innervated via a nerve common with that organ, might contribute a further candidate for a homology with the first unit in Copepoda. This observation of a superficial receptor in an Amphipod furthermore is interesting, as it indicates a sensory character of those structures, distal to the oB, and with connections to the integument, described from numerous Amphipoda, i.e. Ampelisca (Langenbuch, 1928) and Gammarus (Thore, 1932). It also suggests a closer examination of the corresponding structure in Halice (Dahl and Kauri, V).

The innervation of the oB complex

An innervation from the medulla terminalis of the elements in the oB complex is considered to be the rule (cf Hanström, 1947; Gabe, 1966; Kauri, I).

The nerves of the oB complex show a difference regarding the type of neurone processes they contain. Depending on the location of the neurone perikarya, the nerves carry either dendrites or axons. The former is the rule among the nonmalacostracan forms, where the neurone perikarya are located in the medulla terminalis, while the latter type of nerve is found among the Malacostraca. Exceptions from this rule are found among the Anaspidacea and, regarding a few distal elements, also among the Peracarida. The anaspidacean oB has the neurone perikarya located to the ganglionic cell layer, and these are connected with the organ cavities by relatively long dendrites. Among the Peracarida the distal unit of the oB in Boreomysis, which is located in the sensory papilla, (Kauri and Dahl, 1975/III/7) and the sensory pore apparently derive their innervation via dendrites from perikarya close to the proximal unit of the oB. Also the perikarya of the sensory pore neurones among the Decapoda might be located at deeper levels (Chaigneau, 1973 a).

The Anaspidacea also show another characteristic feature, regarding the central connections of the oB nerve. The axons from the sensory perikarya follow three separate nerve tracts. Two of these enter the neuropile of the medulla terminalis, while the third enters the medulla interna (Kauri and Lake, 1972/II/). This latter situation contrasts with the general concept of an innervation from the medulla terminalis. This feature might be shared by a number of other species, as indicated by a preliminary examination of the innervation of the oB complex in Crangon crangon, where also a component from the medulla interna was found to be involved.

However, the medulla interna is evolved from the medulla terminalis (Elofsson and Dahl, 1970), which might explain this special feature of the oB innervation. Nevertheless a further examination of the central connections of the oB nerves is necessary to establish the significance of these observations.

A functional implication might be derived from the small diameters of the oB axons ($0.2\ \mu\text{m}$ - $0.6\ \mu\text{m}$) (Kauri, IV; Dahl and Kauri, V). Such small axon diameters ($0.1\ \mu\text{m}$ - $0.5\ \mu\text{m}$) are interpreted as indicative of chemoreceptors (Laverack, 1974).

Homologies of the oB complex

Introductorily were mentioned the concept of the superficial and deep receptors, included in the oB complex, suggested tentatively. These concepts will be examined here, especially regarding recent information on the fine structure of the individual elements of the oB complex.

The innervation and general location of the component parts of the oB complex, together with the special structural characteristics of the neuronal elements as well as the relations of these neuronal elements with the remaining elements of the component receptors, are considered as especially important characteristics in discussing the homologies of the complex in the Crustacea.

The characteristics of the supporting structures, viz the glial and epidermal elements including the cuticle, as well as the general morphology of the receptors, are considered less important in this relation, as these characteristics partly are readily affected by individual functional demands arising from differences in the morphology of the head and posture of the animal, and partly are subject to variations of a transitory character due to functional demands on the organ itself, eg in relation to the moulting cycle. The differences in the thickness of the cuticular component might be related to the size or habit of the animal, while the presence or absence of pores, at least to an extent, appear to be related to the cuticle thickness, pores having mainly been reported from those forms with a heavier cuticle. These characteristics might have a systematic value when dealing with the lesser taxa, as mentioned in the section on the oB.

Relating the innervation, the present examination has contributed the accentuation of the probable involvement of the medulla interna with the central connections of the nerves from the oB complex and the establishment of the location of the sensory perikarya, which is found to differ between the Malacostraca and the remaining Crustacea. As the medulla interna is derived from the medulla terminalis the variations of the individual relations of the nerves centrally, with the medulla terminalis and medulla interna, are disregarded for the present.

Regarding the location of the neurone perikarya, either to the receptors, the protocerebrum, or in intermediate positions, a possible mechanism of incorporation into the protocerebrum of elements of the oB complex similar to that, shown for frontal organs (Elofsson, 1963), must be considered. From the frontal organs sensory neurones were incorporated into the brain, apparently along with a change of function. However, the situation regarding the oB neurones, known so far, involves no such transformation, as the specific receptory structures have been found to be present in all oB investigated. Although individual oB might be found close to the protocerebrum, or drawn into its ganglionic layer (eg Elofsson, 1971), no reduction of the characteristic oB structure apparently occurs. In discussing the differences in the location levels of the oB structures and mainly those of the neurone perikarya, also functional aspects should be considered, such as availability of space in the anterior part of the head and the length of the oB dendrites. The importance of a common innervation of the superficial receptors and that of the oB must be stressed, while discussing the nature of the former. Information on the proximal connections of the nerves are also necessary in order to evaluate the nature of several superficial receptors, indicated from light microscopical investigations, eg in Anaspides (Kauri and Lake, 1972/II/) and in Squilla (Hanström, 1947).

The information on the location of the receptors of the oB complex, that has been brought into the discussion by the present investigation, merely confirms a location to the anterior part of the head or to the eye stalks, thus corroborating the previous concept.

The special structural characteristics of the deep receptors relate to the oB units, which have been found in all species examined. The individual elements of the units have been shown to have corresponding interrelations. The significant differences are found in the special structural characteristics of the sensory neurones. Apart from differences in the length of dendrites, and occasional differences in the cytoplasmic characteristics, the cilia and ciliary derivatives show the more important characteristics. Of these the number of cilia and type of ramification are discussed. The Copepoda, due to the multiciliated dendrites, have a quite distinct oB. The types of ramification, viz the tubular, the lamellar with onion bodies, and the tubular/lamellar (without characteristic onion bodies), are distributed as follows. The tubular type is found in the non-Malacostraca possessing oB, and are also found in the Peracarida

The tubular/lamellar type is characteristic of the Anaspidacea, but is also reported from a few Decapoda. The lamellar type with onion bodies, finally, is characteristic for the Decapoda, Stomatopoda, Leptostraca and probably the Euphausiacea. The tubular/lamellar type is intermediate structurally between the other two types. The occurrence of this type among the Decapoda, as indicated in the present examination, must be evaluated with caution, until further examinations are available. If this type of deep receptor, however, is established, dual functions on this level are indicated among the Decapoda.

The information, presented on the superficial receptors so far, represents relatively few taxa. The number of different receptors on the superficial level cannot be established from the material presented so far, but at least a dual character is to be expected, as indicated by the presence of two different sensory structures among individual species of the Decapoda, Copepoda, and probably the Cirripedia, and Leptostraca. Nevertheless one type of receptor emerges, with a sufficiently uniform fine structural detail. As in the oB, rather a wide range of specialized cilia will have to be accommodated. The organ described from the Mysidacea, with its relatively simple structure, comes closest to a basic definition of this receptor and is also best compared to the cavity receptors found among the Maxillopoda, especially the Copepoda, and Anostraca thus paralleling the comparison of the oB of this species to that of the non-Malacostraca. This organ also compares favourably to the main sensory pore among Decapoda.

Elofsson and Lake (1971) formulate the known characteristics of the cavity receptor in the Anostraca, namely "1. ciliated neurons, which end in 2. a cavity, beneath the cuticle and it is known 3. that the organs emanate from the medullae terminales".

This concept is here widened, summarizing the characteristics of the oB complex discussed above, to comprise also the deep receptors of the oB complex: (1) an extracellular cavity with (2) ciliated neurones, which (3) proximally connect to the medulla terminalis, or a corresponding location in the protocerebrum.

The superficial and deep receptors then are characterized by individual criteria: (4 a) superficial receptors have cavities, distally bordered by elements of the integument (4 b) deep receptors have cavities formed by bordering glia.

Between them the characteristics under 1 - 3, as discussed here, through their constancy satisfy the homology criteria of location and special structural characteristics of the oB complex (Remane, 1961).

The individual criteria for the receptors on the superficial and deep levels contribute the additional characteristics of special structure for the establishment of the homologies on both levels individually.

The discussion of the fine structural characteristics of the receptors in the oB complex thus corroborates the homologizations made previously from light microscopical material including the concept of the oB complex with its superficial and deep receptors. It also demonstrates an interesting variation within the two homologous systems, the deep and the superficial, which will have to be examined further, before the full significance of the structural characteristics can be established. The variation of the structural characteristics of the oB during the phases of the moulting cycle are not fully known eg. Also the significance of the neurosecretory elements found close to the oB units in the Decapoda Brachyura should be established (Smith, 19

The terms superficial receptor and deep receptor should be used as neutral terms to designate receptor levels, and not in lieu of established, adequate terms. Thus the term oB should be used for the receptors on the deep level.

On the superficial level the nomenclature is more heterogenous, comprising terms such as frontal filament, sensory pore, main sensory pore, lateral sensory pore, eye papilla, sensory papilla, and cavity receptor. Of these the term papilla probably is inadequate, as discussed above (section on superficial receptors), and the frontal filament is a specialized receptor. The sensory pore probably will turn out to be a rather heterogenous concept with intricate subdivisions, and as such difficult to handle. The term cavity receptor finally was the first to be defined ultrastructurally, and also carries specific information on one type of superficial receptor, which probably will be found more generally. It therefore seems appropriate to use this term for the superficial receptors described from Artemia, Boreomysis, and the Copepoda. Also the main sensory pore in Atyaephyra should be included under this term.

This is made notwithstanding the diagnose for the oB receptors proposed above, implicating that the term cavity receptor would cover all the receptors of the oB complex. This suppression is justified further as the deep receptors so far comprise only one, well established receptor, the oB.

Further specification of the remaining superficial receptors will not be attempted, as information still is too scarce on their ultrastructure, and thus their affinities difficult to establish. For these receptors terms of the sensory pore type probably would be most appropriate until adequate terms are established.

Functional considerations

Neurosecretion. The oB has been conceived to have a neurosecretory function. This mainly came about as a result of interpretations from two staining techniques, utilizing chrome-haematoxylin phloxin (Gomori, 1941), and paraldehyde-fuchsin (Gabe, 1953). Secretory products from neurosecretory cells in the hypothalamus and in the groups of neurosecretory cells in the brain and primary optic centra of arthropods gave positive reactions to the chrome-haematoxylin and paraldehyde-fuchsin. Positive reactions were also obtained in the sinus gland and the organ of Bellonci. Partly these interpretations also were encouraged by extirpation experiments (eg Humbert, 1965; Daguerre de Hureux, 1967), where extirpation of the oB resulted in effects on chromatophores eg, similar to those obtained in sinus-gland extirpated specimens.

It must be pointed out that already Hanström (1947) was reluctant to ascribe a neurosecretory function to the oB without reservations. Later Gabe (1966) in discussing the staining methods, mentioned, found their specificity for neurosecretory products rather low. He also reported a large material of histological observations on the oB and came to the conclusion that this organ was not active in neurosecretion. These findings have been corroborated more recently by the information reported on the fine structure of the organ, rendering the neurosecretory concept further in doubt and revealing an organ of sensory characteristics. It is concluded that the oB is a sensory organ with a strong secretory activity other than neurosecretion (Chaigneau, 1971 a; Elofsson, 1971; Lake and Ong, 1972; Kauri and Dahl, 1975/III/; Kauri, IV). A similar situation apparently is found in the cavity receptor of the oB complex (cf Elofsson and Lake, 1971).

Only from the *Brachyura* there are found neurosecretory elements in connection with the oB. Thus Smith (1974) reported two types of neurosecretory neurones from the oB in *Carcinus maenas*. Neither of these cells apparently are connected with the oB, but it is difficult to get a clear impression of the spatial relationships from the description given. Most probably these cells do not belong to the oB units, but to the interstitial tissues. A careful examination of the fine structure of the oB units in *Crangon* and *Leander* (Kauri, unpubl.) failed to reveal any neurosecretory elements directly related to the oB units of these decapods.

The functional unit of the oB. The oB units (Fig 1,3) constitute the functional units of the organ. The two cellular elements, the bordering glia and the neurone terminals with their cilia contribute the functional organelles.

The intimate relations between elements from these two cells have been referred to (cf Pl 1 B; Pl 2 B; Pl 3 D). Most probably the trophospongium in the neurone terminals contributes to the metabolism in this region, extremely rich in mitochondria. The situation is reminiscent of that seen in the ellipsoid of the retinal receptors (cf Barber, 1974), and a production of energetic compounds is indicated, cf the distribution of mitochondria in ion-transporting cells eg (Munn, 1974).

In *Halice* (Dahl and Kauri, V) a distribution of vesicles was found in the region of basal ciliary structures and also in the ciliary shaft with accumulations of vesicular material in the ramifications. Similar electron lucent vesicular material has been found in sensory cilia in *Balanus* (Kauri, I), *Crangon* (Pl 2 B), *Carcinus* (Smith, 1974), in *Sphaeroma* (Chaigneau, 1971 a), and in *Insecta Homoptera* (Marshall, 1973). Marshall lists further occurrence of vesicular material and discusses a transport mechanism into the cilium, through the neck region, possibly a transport facilitated by the microtubular component in the cilium (cf Marshall, 1973; Nadelhaft, 1974). Relations between rootlets and endoplasmic reticulum have been discussed in the context of ciliary metabolism (Cordier, 1976). In the oB neurones the cilia have one basal body each, and two cilia usually are found on each dendrite. The insect sensillum often has an accessory centriole located axially proximal to the basal body. There is only one cilium (eg Marshall, 1973). Considering the possible role in the transport of nutrients via the ciliary neck a rather important transport function might lie with the basal apparatus apart from the anchoring function and that of controlling repair of distal sensory endings (Laverack, 1974). Transport of protein through the cilium has been shown by autoradiographic methods (Young, 1968; Young and Bok, 1969).

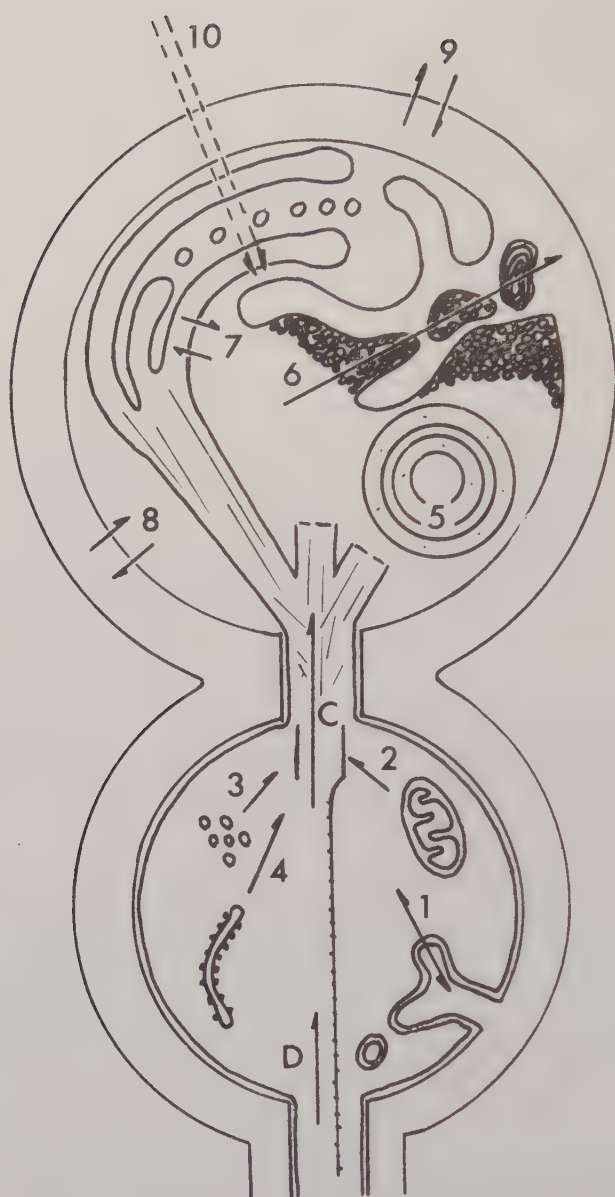


Fig 3 Functional unit of the oB. Diagrammatic representation of hypothetical trophic relations. The diagram is based on observations from several species. Dendritic swelling in lower part of figure comprises dendritic transport (D), trophospongium (1), mitochondria and transport of energetic compounds (2), vesicular material (metabolite or membrane transport) (3), rough endoplasmic reticulum and protein transport (4), and basal ciliary apparatus with rootlet. The ciliary transport (C) is thought to be continued distally via more or less evenly distributed microtubules (shown in sectioned onion body, 5). The vesiculated ciliary lamellae are phagocytized and digested via lytic processes in the bordering glia (6). Part of the maintenance of the sensory membranes occurs via the cavity liquor (7), which is controlled via the bordering glia (8). The bordering glia regulates the trophic relations with the haemocoel (9). Sensory impulses penetrate to the sensory membranes (10). For references and a discussion relating to the individual processes, see the text.

Distally in the cilium and its ramifications there always occur microtubules in an even distribution relative to the ciliary surface. Apart from cytoskeletal functions, this condition also indicates a possibility of further transport of metabolites after arriving into the ciliary shaft. The situation in the often enormously ramified sensory cilia contrasts with that in the microvillar receptors (eg in the vomero-nasal organ, Graziadei, 1971). This might be an indication of the value of a ciliary basal structure regarding the "carrying capacity" of sensory membrane.

A turnover of olfactory elements has been shown in aquatic vertebrates (Thornhill, 1967), and of whole olfactory neurones in terrestrial vertebrates (cf Graziadei, 1974). For reticular rods a turnover of the membrane material of the outer segments has been demonstrated (Young and Bok, 1969). The fate of discarded receptor material might be a direct loss of membranes to the exterior in olfactory receptors as in Coleoptera (Ernst, 1972), Ostracoda (Andersson, 1975). A similar mechanism might be operating in the superficial receptor in Doropygus, as described by Dudley (1972). In receptors on deeper levels macrophages phagocytize the material, as in the frog pineal (Bunt and Kelly, 1971), or it might be phagocytized by the pigment epithelium, as in the retinal rods (Young and Bok, 1969). For the retinula cells in Palaemonetes a flow chart has been presented regarding the turnover of sensory membranes (Itaya, 1976). The entire process is thought to take place around and in the reticular cells. The turnover for the vertebrate olfactory receptors has been estimated to about 2 -3 weeks (Graziadei, 1974), and for the retinal rod outer segments to about two months (Young and Bok, 1969).

The indications of the possible phagocytic activity in the bordering glia cells have been observed in several preparations of Leander, Crangon (Pl 2 B), and Derocheilocaris (Kauri, I). The included vesicular material from the lamellar vesiculation is clearly identified in the vacuoles of the bordering glia. If this process can be verified, there is present in the oB a mechanism analogous to those found in the receptors related above. This is interesting, as it indicates common mechanisms and apparently rather high metabolic activity in receptors from distant species. The indication of high metabolic activity is interesting as it implies a need for metabolites and a possible explanation of the strong staining reactions in the oB cavity.

This turnover on the ciliary level might be paralleled by one of entire neurone turnover, as indicated by Chaigneau (1971 a). Observations, similar to those made by Chaigneau, have been recorded from material of Crangon and Leander (Kauri, unpubl.). Also similar observations have been made in Diastylis (Kauri, IV).

The absence of phagocytic indications in eg the larvae of Balanus might indicate that the span of life of these larvae is too short to need a turnover.

The receptor cavity, as an internal milieu of specific characteristics, carefully controlled, has been stressed by Zacharuk (1971). A continuous production of the liquor in the receptor cavity is suggested by Steinbrecht (1974), at least in sensillae with pores. He also indicates a relatively high activity in those cells bordering to the cavity. A situation of similar characteristics exists in the oB cavity, where the internal milieu obviously will have to be controlled to encertain proper sensory function, and where the apparently active bordering glia occupies the natural position for carrying out such a control.

Regarding the sensory function of the receptors in the oB complex, the information is very sparse. Few experimental investigations have been carried out.

The superficial receptors most authors consider to be chemosensory, as indicated by thin cuticle, often in combination with pores, and a ciliation reminiscent of chemosensory structures in Insecta (Elofsson, 1971; Dudley, 1972; Chaigneau, 1973 a; Walker, 1974). However, also mechanoreception is considered.

For the deep receptors a wide range of functions has been suggested. Photo- and chemoreception being two of those discussed most, but pressure, infrared, and photoperiod registration are other interesting possibilities (Chaigneau, 1971 a, 1973 b, 1975; Elofsson, 1971; Dudley, 1972; Lake and Ong, 1972; Smith, 1974; Walker, 1974). It is not intended to discuss these hypotheses more closely here. The ultrastructural similarities of the receptors with onion bodies appear to be with photoreceptors among the vertebrates, especially the type of receptors found in the pineal organ (eg R  deberg, 1971). The receptors with tubularly branching cilia have structural characteristics which in most cases have been associated with chemoreceptors, although the affinities to certain ciliary photoreceptors are recognized (cf Barber, 1974).

The extirpation experiments carried out by Humbert (1965) and Daguerre de Hureux (1967) on Palaemon serratus and Sphaeroma serratum respectively, contributed similar results from both species and regardless if the oB or the sinus gland were extirpated. The latter extirpation gave the strongest response, and gave it faster. Effects were registered on a number of functions, among them moult acceleration. At the time a direct transport of hormone precursors was suggested from the oB to the sinus gland. For the present two possible explanations might be conceived. Either the oB really releases a hormone (cf below) or it influences the sinus gland via the CNS. In both cases the effect must be localized to a function, important enough to bring about the diversity of secondary effects, observed by Humbert and Daguerre de Hureux. Such effects might be eg a direct stimulation of the moulting cycle, or a registration of changes in the photoperiod by the oB.

Chaigneau and Juchault (1974) in the protandric parasite Anilocra frontalis demonstrate a hormone release from the bordering glia (intercalated cells) of the oB. They also indicate the possibility of a chemoreception in that species of a "pheromone-like" substance.

The function of the oB complex on both levels still is practically unknown, but certain indications are emerging. Certainly both types of receptors appear to perform important functions, as indicated by their large size in many species.

Conclusions

A homologous organ of Bellonci (oB) complex has been established, comprising receptors which have an extracellular cavity with ciliated neurons, proximally connecting to the medulla terminalis, or a corresponding location in the protocerebrum.

The oB complex has one homologous superficial system of receptors, with cavities, distally bordered by elements of the integument, and one homologous deep system of receptors, which have cavities formed by bordering glia.

A relatively high metabolic level in the individual oB units with interactions between the bordering glia and sensory neurone components is concluded from the fine structural characteristics of the component elements.

References

- Amar, R. 1950. Les formations endocrines cérébrales des Isopodes marins. C.R. Acad. Sci. Paris. 230:407-409.
- . 1951. Formations endocrines cérébrales des Isopodes marins et comportement chromatique d'*Idotea*. Ann.Fac. Sci. Marseille. 220:171-305.
- Andersson, A. 1975. The Ultrastructure of the Presumed Chemoreceptor Aesthetasc "Y" of a Cypridid Ostracode. Zool. Scr. 4:151-158.
- Barber, V.C. 1974. Cilia in sense organs. In: Cilia and flagella. Sleight, M.A. (ed). Academic Press. London. 403-433.
- Bellonci, G. 1881. Sistema nervoso e organi dei sensi dello Sphaeroma serratum. Atti Accad. Real. Lincei. 10:91-103.
- Bunt, A. Heffington, Kelly, D.E. 1971. Frog Pineal Photoreceptor Renewal: Preliminary Observations. Anat. Rec. 171:99-116.
- Chaigneau, J. 1969. Etude ultrastructurale de l'organe de Bellonci de Sphaeroma serratum (Fabricius), Crustacé Isopode Flabellifère. C.R. Acad. Sci. Paris. 268:3177-3179.
- . 1971 a. L'organe de Bellonci du Crustacé Isopode Sphaeroma serratum (Fabricius). Ultrastructure et signification. Z. Zellforsch. 112:166-187.
- . 1971 b. Etude préliminaire de l'ultrastructure des corps en bulbe d'oignon présents dans l'organe de Bellonci de certain Crustacés. Observations faites chez Palaemon elegans Rathke, Crustacé Décapode Natantia. C.R. Acad. Sci. Paris. 272:303-306.
- . 1972 a. Observation ultrastructurale de l'organe de Bellonci de la larve de Squilla mantis Latreille, Crustacé Stomatopode. C.R. Acad. Sci. Paris. 274:1697-1700.
- . 1972 b. Particularités ultrastructurales de l'organe de Bellonci d'Anilocra frontalis Milne Edwards, Crustacé Isopode Flabellifère Cymothoide. C.R. Acad. Sci. Paris. 274:1194-1197.
- . 1973 a. Fine Structure of the Sensory Pore Present in the Eyestalk of Crustacea Natantia. Z. Zellforsch. 145:213-227.

Chaigneau, J. 1973. b.

Données ultrastructurales sur le complexe pore sensoriel-organe de Bellonci de Nebalia bipes Fabricius Crustacé Leptostracé. C.R. Acad. Sci. Paris. 276:1753-1756.

— . 1975.

Ultrastructure de l'organe de Bellonci d'un Crustacé Décapode Natantia vivant dans le milieu souterrain. C.R. Acad. Sci. Paris. 280:1131-1134.

— ., Juchault, P. 1974.

Evolution ultrastructurale en relation avec l'état sexuel, de l'organe de Bellonci autochtone et implanté, chez le Crustacé, Isopode hermaphrodite Anilocra frontalis. C.R. Acad. Sci. Paris. 279:77

Claus, C. 1863.

Die frei lebenden Copepoden mit besonderer Berücksichtigung der Fauna Deutschlands, der Nordsee und des Mittelmeeres. Wilhelm Engelmann, Leipzig.

Cordier, A.C. 1976.

Relationship between Ciliary Rootlets and Smooth Endoplasmic Reticulum. Cell. Tiss. Res. 166:315-3

Daguerre de Hureux, N. 1967.

Etude expérimentale du rôle de l'organe de Bellonci et du lobe optique sur le comportement chromatique et la mue de Sphaeroma serratum. Incidence des ablations sur son comportement sexuel. Bull. Soc. Sci. Nat. Phys. du Maroc. 47:33-115.

Dahl, E. 1963.

Main evolutionary lines among recent Crustacea. In: Phylogeny and evolution of Crustacea. Museum of Comparative Zoology, Special Publ. Ed. H.B. Whittington and W.D.I. Rolfe. 1-26.

— . 1965.

Frontal organs and protocerebral neurosecretory systems in Crustacea and Insecta. Gen. Comp. Endocrinol. 5:614-617.

— ., Kauri, T./V

Observations on the fine Structure of the Organ of Bellonci (SPX) in Halice abyssii BOECK (Crustacea Peracarida, Amphipoda).

Dohrn, R. 1906.

Die Nervenendigung in Sinnesnervenzellen eines Schizopoden. Zool. Anz. 29:347-352.

Drach, P., Gabe, M. 1960.

Diversité structurale de l'organe X (pars distale) chez les Crustacés Décapodes. Bull. Soc. Zool. France. Paris. 85:199.

Dudley, P.L. 1969.

The fine structure and development of the nauplius eye of the copepod Doropygus seclusus Illg. Cellule. 68:7-42.

— . 1972.

The Fine Structure of a Cephalic Sensory Receptor in the Copepod Doropygus seclusus Illg (Crustacea Copepoda: Notodelphidae). J. Morph. 138:407-432.

Elofsson, R. 1963.

The nauplius eye and frontal organs in Decapoda (Crustacea). Sarsia. 12:1-68.

— . 1965.

The nauplius eye and frontal organs in Malacostraca (Crustacea). Sarsia. 19:1-54.

— . 1966.

The nauplius eye and frontal organs in the non-Malacostraca (Crustacea). Sarsia. 25:1-128.

- Elofsson, R. 1971. The Ultrastructure of a Chemoreceptor Organ in the Head of Copepod Crustaceans. *Acta Zool.* 52:299-315.
- , Dahl, E. 1970. The Optic Neuropiles and Chiasmata of Crustacea. *Z. Zellforsch.* 107:343-360.
- , Lake, P. 1971. On the Cavity Receptor Organ (X-Organ or Organ of Bellonci) of *Artemia salina* (Crustacea; Anostraca). *Z. Zellforsch.* 121:319-326.
- Gabe, M. 1953. Quelques applications de la coloration par la fuchsine-paraldéhyde. *Bull. Micr. appl.* 3:153-162.
- . 1966. Neurosecretion. Pergamon Press. Oxford.
- Gamroth, A. 1878. Beiträge zur Kenntnis der Naturgeschichte der Caprellen. *Z. wiss. Zool.* 31:100-123.
- Gomori, G. 1941. Observations with differential stains on human islets of Langerhans. *Am. J. Path.* 17:395-406.
- Graziadei, P.P.C. 1971. The Olfactory Mucosa of Vertebrates. In: *Handbook of Sensory Physiology*. IV:1. Beidler, L.M. (ed). Springer-Verlag. Berlin.
- . 1974. The olfactory and taste organs of vertebrates: a dynamic approach to the study of their morphology. In: *Transduction Mechanisms in Chemoreception*. Poynder, T.M. (ed). Information Retrieval Limited. London. 3-14.
- Hanström, B. 1931. Neue Untersuchungen über Sinnesorgane und Nervensystem der Crustaceen. 1. *Z. Morph. ökol. Tiere.* 23:80-236.
- . 1933. Neue Untersuchungen über Sinnesorgane und Nervensystem der Crustaceen. 2. *Zool. Jb. Anat.* 56:387-520.
- . 1934. Neue Untersuchungen über Sinnesorgane und Nervensystem der Crustaceen. 4. *Ark. Zool.* 26 A (24):1-66.
- . 1947. The brain, the sense organs and the incretory organs of the head in the Crustacea Malacostraca. *Acta Univ. Lund., N.F.* 58 (9): 1-45.
- Hogstad, A.-M. 1969. The X organ and the sinus gland of *Mysis relicta* Lovén (Crustacea: Mysidacea). *Nytt Mag. Zool.* 17:105-109.
- Humbert, C. 1965. Étude expérimentale du rôle de l'organe X (pars distalis) dans les changements de couleur et la mue de la crevette *Palaemon serratus*. *Trav. Inst. scient. chérif., sér. Zool.* 32.
- Jacques, F. 1969. Histogenèse des pédoncules oculaires des larves de Stomatopodes. *Vie et Milieu.* (A) 20:565-593.
- Kauri, T. 1966. On the sensory papilla X organ in cirriped larvae. *Crustaceana*, 11:115-122.

- Kauri, T./I. The fine structure of the organ of Bellonci in the Crustacea Maxillopoda, especially Balanus improvisus Darwin (Maxillopoda Cirripedia) and Derocheilocaris remanei Delamare and Chappuis (Maxillopoda Mystacocarida).
- . /IV. The fine structure of the organ of Bellonci in Diastylis rathkei Kr. (Crustacea, Peracarida, Cumacea).
- ., Dahl, E. 1975/III Fine Structure of the Organ of Bellonci (SPX) in Boreomysis arctica (Krøyer) (Crustacea, Mysidacea). Zool. Scr. 4:41-47.
- ., Lake, P.S. 1972/II The Structure of the Organ of Bellonci of the Syncarid Crustacean, Anaspides tasmaniae (Thomson). Z. Zellforsch. 132:431-450.
- Lake, P.S., Ong, J.E. 1972. Observations of the organ of Bellonci of the shrimp Paratya tasmaniensis Riek (Crustacea: Decapoda: Atyidae) with particular reference to the structure of the onion body cells. Aust. J. Zool. 20:215-234.
- Langenbuch, R. 1928. Über die Statocysten einiger Crustaceen. Zool. Jb. Allg. Zool. 44:575-622.
- Laverack, M.S. 1974. The structure and function of chemoreceptor cells. In: Chemoreception in Marine organisms. Grant, P., Mackie, A.M. (eds). Academic Press. London. 1-48.
- Marshall, A.T. 1973. Vesicular structures in the dendrites of an insect olfactory receptor. Tissue and Cell. 5:233-241.
- Munn, E.A. 1974. The Structure of Mitochondria. Academic Press. London.
- Nadelhaft, I. 1974. Microtubule densities and total numbers in selected axons of the crayfish abdominal nerve cord. J. Neurocyt. 3:73-86.
- Neville, A.C. 1975. Biology of the Arthropod Cuticle. Springer-Verlag. Berlin.
- Pickett-Heaps, J.D. 1969. The evolution of the mitotic apparatus: an attempt at comparative ultrastructural cytology in dividing plant cells. Cytobios. 3:257-280.
- Pitelka, D.R. 1974. Basal bodies and root structures. In: Sleigh, M.A. (Ed). Cilia and Flagella. Academic Press. London. 437-469.
- Remane, A. 1961. Gedanken zum Problem Homologie und Analogie, Praeadaptation und Parallelität. Zool. Anz. 165:447-465.
- Rüdeberg, C. 1971. Structure of the Pineal Organs of Anguilla anguilla L. and Lebistes reticulatus Peters (Teleostei). Z. Zellforsch. 122:227-243.
- Scharrer, E. 1964. A specialized trophospongium in large neurons of Leptodora (Crustacea). Z. Zellforsch. 61:803-812.

- Smith, G. 1974. The Ultrastructure of the Organ of Bellonci of Carcinus maenas (Crustacea: Decapoda). Cell Tiss. Res. 155:127-134.
- Steinbrecht, R.A. 1974. Morphology of insect chemoreceptors. In: Transduction mechanisms in Chemoreception. Poynder, T.M. (ed). Information Retrieval Limited. London. 15-24.
- Ståhl, F. 1938. Über das Vorkommen von inkretorischen Organen und Farbwechselhormonen im Kopf einiger Crustaceen. Acta Univ. Lund. NF (2) 34 (12):1-20.
- Thore, S. 1932. Über Statocysten und Frontalorgane bei Gammarus pulex und Gammarus locusta. Zool. Jb. Anat. 55:489-504.
- Thornhill, R.A. 1967. The ultrastructure of the olfactory epithelium of the lamprey Lampetra fluviatilis. J. Cell Sci. 2:591-602.
- Walker, G. 1974. The Fine Structure of the Frontal Filament Complex of Barnacle Larvae (Crustacea: Cirripedia). Cell Tiss. Res. 152:449-465.
- Young, R.W. 1968. Passage of Newly Formed Protein through the Connecting Cilium of Retinal Rods in the Frog. J. Ultrastr. Res. 23:462-473.
- , Bok, D. 1969. Participation of the retinal pigment epithelium in the rod outer segment renewal process. J. Cell. Biol. 42:392-403.
- Zacharuk, R.Y. 1971. Fine structure of peripheral terminations in the porous sensillar cone of larvae of Ctenicera destructor (Brown) (Coleoptera, Elateridae), and probable fixation artefacts. Can. J. Zool. 49:789-799.

PLATES 1 - 3

Note on material and method

The material was obtained as follows: Leander adspersus and Crangon crangon from the Sound, Pandalus borealis from the Kristinebergs Zoologiska Station, Fiskebäckskil, Sweden, and Boreomysis arctica from Biologisk Stasjon, Espesgrend, Norway. The preparations, and processing procedures were similar to those used for the oB in Boreomysis (Kauri and Dahl, 1975). The oB from Pandalus (Pl. 3:A) was prefixed in formaldehyde-glutaraldehyde (Karnovsky, 1965).

The SEM preparation (Pl. 3:B) was carried out using the technique of critical point drying in CO₂ (Boyde and Wood, 1969). The sections were examined in Philips EM 300 or Zeiss EM 10.

Boyde, A., Wood, C. 1969. Preparation of animal tissues for surface-scanning electron microscopy. J. Microsc. 90:221-249.

Karnovsky, M.J. 1965. A formaldehyde-glutaraldehyde fixative of high osmolarity for use in electron microscopy. J. Cell Biol. 27:49 A.

Kauri, T., Dahl, E. 1975. Fine Structure of the Organ of Bellonci (SPX) in Boreomysis arctica (Krøyer) (Crustacea, Mysidacea). Zool. Scr. 4:41-47.

Plate 1

A Crangon crangon. Intracellular capillary close to oB unit.

1 - capillary lumen; 2 - ciliary lamellae in oB unit. Index 1 μm .

B Leander adspersus. Supporting cell in oB with process (1) penetrating into a neurone perikaryon (2). Index 0,5 μm .

C Crangon crangon. Intralamellar vesiculation (arrows) in oB. 1 - neurone perikaryon; 2 - supporting cell. Index 1 μm .

D Crangon crangon. Interlamellar vesiculation (solid arrows) in oB. Open arrows - microtubules; 1 - supporting cell process. Index 1 μm .

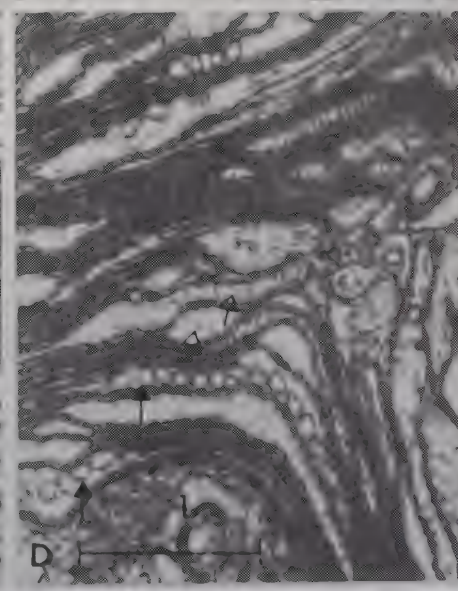
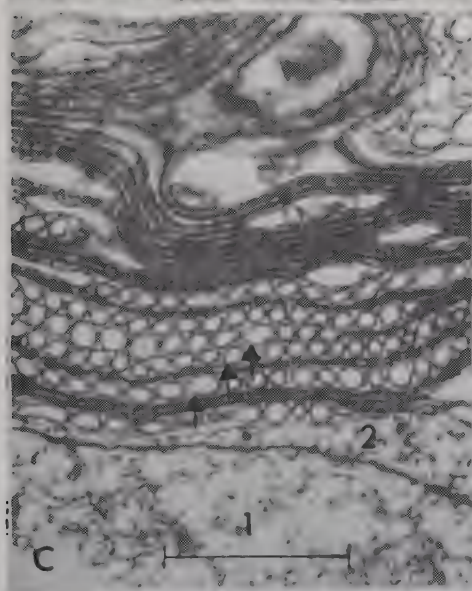
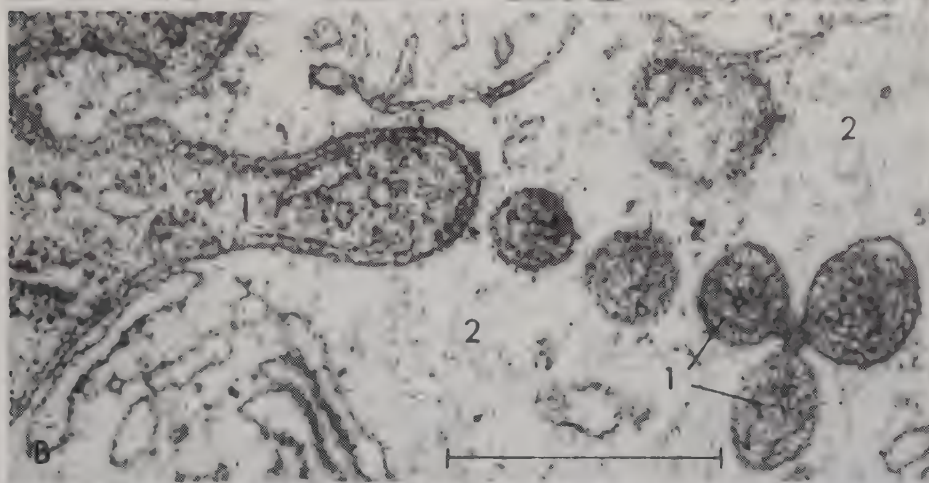
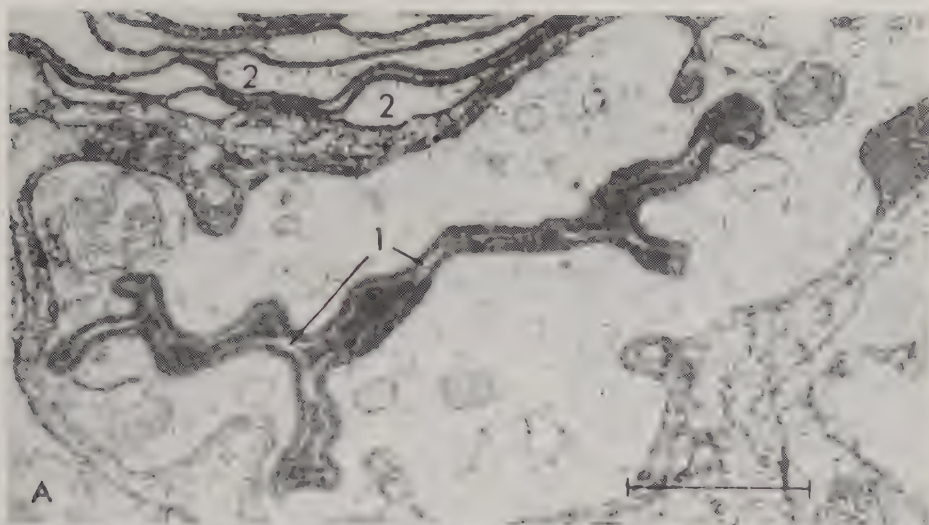


Plate 2

A Leander adspersus. Supporting cell process (1) with ribosomes, mitochondria, and thin plasma membrane (arrows) in oB. 2 - vesiculated material in organ cavity; 3 - supporting cell; 4 - neurone perikaryon. Index $1\mu\text{m}$.

B Crangon crangon. Supporting cell process in oB with inclusions of vacuolar material (1) and myeloid figures (2). open arrows - microtubules of ciliary lamella; solid arrows - supporting cell cytoplasm between inclusions; 3 - vesicular material of ciliary lamella. Index $1\mu\text{m}$.

C Boreomysis arctica. Bordering cell (1) with denser material locally in membrane (arrows). 2 - granular material in cavity. Index $0,5\mu\text{m}$.

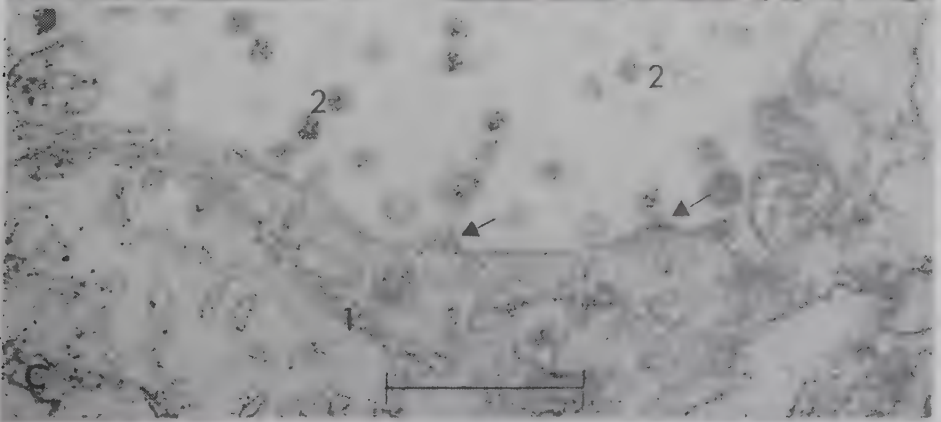
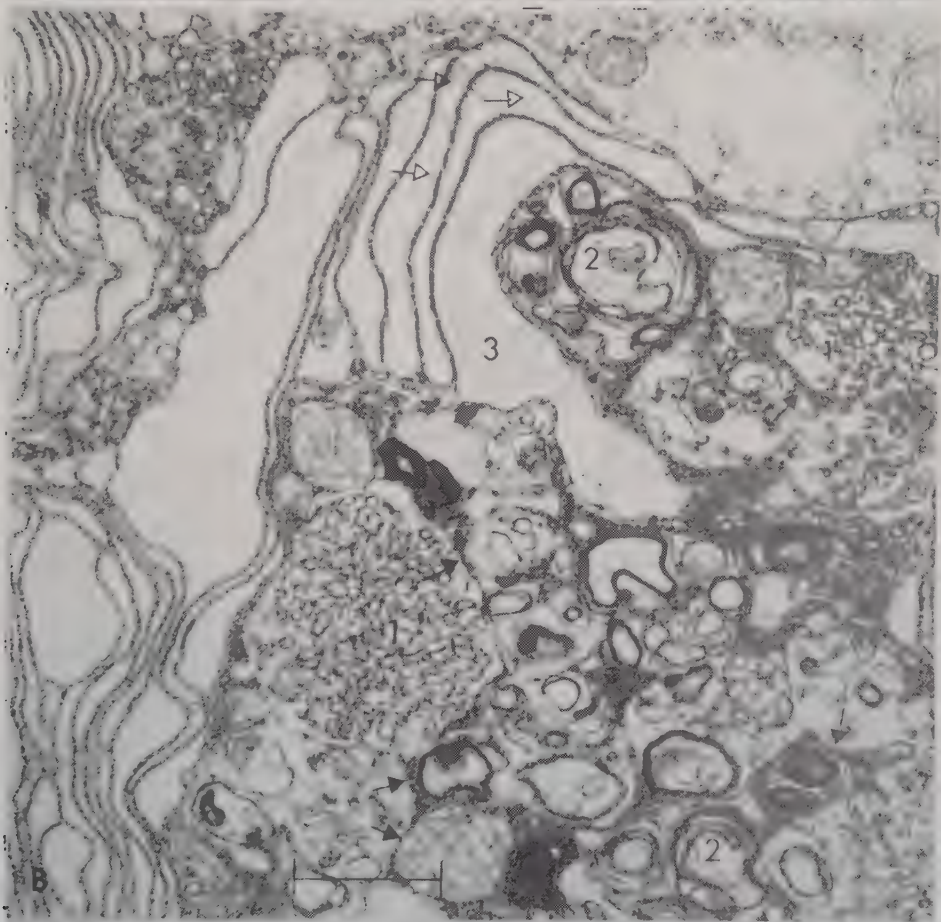
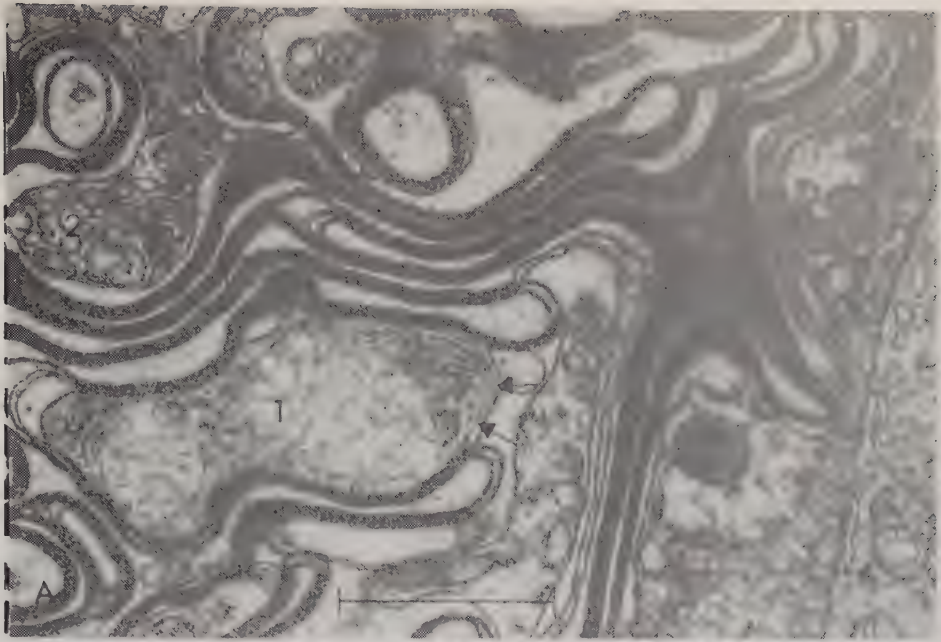


Plate 3

A Pandalus borealis. Atypical unit in oB. 1 - cavity; 2 - ciliary shafts; 3 - ciliary lamellae; 4 - dendrite with pair of rootlets; 5 - glial cell; 6 - supporting cell; 7 - haemocoel. Index, 5 μm .

B Boreomysis arctica. Sensory papilla with occasional "pores" (arrows). SEM. Index, 2,5 μm .

C Boreomysis arctica. Sensory papilla, sectioned perpendicular to the surface. 1 - cuticle; 2 - processes of epidermal cells with microvilli underlying the cuticle (arrows). Index, 0,5 μm .

D Boreomysis arctica. Dendritic termination (1) in sensory pore with ciliary rootlet (2), neck (3), and shaft (4). 5 - tubular ciliary ramifications; 6 - supporting cell. Note the microtubules in the ciliary shaft. Index, 0,5 μm .

